GRAY WOLVES ADJUST THEIR SPATIAL AND SOCIAL ENVIRONMENTS ACCORDING TO PREY DISTRIBUTIONS IN A MULTI-PREY SYSTEM

by

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ABSTRACT

Animals modify their environment through movement to increase their success in acquiring energy. This may be done by selecting spaces to increase encounter rates with prey through different space use tactics, or in the case of social carnivores, adjusting social environments to balance the tensions associated with capturing prey and sharing the acquired energy with conspecifics. I tested hypotheses on how social predators select space based on three prey distribution metrics, and how they subsequently adjust their level of cohesion with conspecifics based on prey distribution. I tested these hypotheses in Riding Mountain National Park, Manitoba, a multi-prey system where gray wolves (*Canis lupus*) prey on moose (*Alces alces*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*) and beaver (*Castor canadensis*). I found evidence that wolves used the predicted space use tactic for their primary prey species and adjust their level of cohesion based on the distribution of moose and beaver.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ΔAIC – Change in Akaike's Information Criterion

AIC – Akaike's Information Criterion

Bovine TB – Bovine Tuberculosis

CDV – Canine Distemper Virus

CI – Confidence Interval

EF – Effect size

GPS – Global positioning system

MCP – Minimum convex polygon

RMNP – Riding Mountain National Park

RSF – Resource selection function

LIST OF APPENDICES

CHAPTER 1: PROLOGUE

1.1 General Introduction

Animals do not passively exist in space, but actively modify their environment through movement to increase their success in acquiring energy (Charnov 1976). This energy is acquired by capturing prey, be it plant species for herbivores or other animals for carnivores. An animal's spatial environment is rarely uniform, and ecosystems are often heterogeneous matrices of landscapes and habitats, where resources are not distributed equally across the landscape (Turner 1989). According to the functional response theory, encounter rates between predators and prey increase with increasing prey density (Holling 1959). Therefore, animals modify their spatial environment by selecting space where they have higher chances of encountering prey, thus increasing their success in acquiring energy (Mittelbach 1981). Although density is a fundamental component of encounter rates, other landscape factors such as habitat preference (Kittle et al. 2017) and prey vulnerability (Grant et al. 2005) also contribute to encounter rates between predator and prey.

In addition to modifying their spatial environment to their benefit, predators may alter their social environment to trade off prey acquisition and resource partitioning among conspecifics. In some cases, individuals avoid conspecifics due to competition for resources, be it through direct or indirect competition (Janssen et al. 1997, Cubaynes et al. 2014). However, in species such as social carnivores, cooperation may allow for more opportunities to utilize resource that would otherwise not be accessible, such as capturing larger prey species (MacNulty et al. 2014). How social carnivores select space to find

their prey, and how they cooperate depending on the prey species are two important facets of the same hunting behaviour. Therefore, how the distribution of resources on the landscape affects the interplay between how individuals modify their spatial and social environments is a key component that has been overlooked in ecology.

In terms of resources, predators alter space use patterns to gain access to their resource (i.e., prey) (Kittle et al. 2015, 2017). Prey species have different distributions on the landscape, ranging from large gregarious groups, to solitary with even distribution across the landscape. Predators may use different tactics to effectively track prey based on their different spatial distributions on the landscape. Additionally, the tactics employed may also vary as a function of anti-predator behaviours (Mitchell and Lima 2002, Taraborelli et al. 2012, Sand et al. 2016). For example, predator space use may be explained by the prey abundance, where predators select to be in areas where prey are most abundant (Weckel et al. 2006, Shepard and Lambertucci 2013). Predator space use may also be explained by the prey habitat, where predators select to be in habitats preferred by their prey (Williams and Flaxman 2012, Latham et al. 2013). Finally, predator space use may be explained by the prey catchability by selecting for areas where prey are more vulnerable to predation (Patterson and Messier 2001, Hebblewhite et al. 2005, Davidson et al. 2012). Furthermore, these tactics become increasingly complex in a multi-prey system where predators use different tactics to capture prey based their specific distribution and anti-predator traits of specific prey species (Kittle et al. 2017). The co-occurrence of different prey species in a system adds to the heterogeneity of the landscape. Predators need to adjust their hunting tactics to balance out the likelihood of

encountering different prey species that occur in different habitats and have different energetic contents. Generalist predators that target multiple prey species could simultaneously use different strategies for each prey species. For example; a predator in a multi-prey system may track a prey species that aggregates in large herds by selecting areas of high prey density, while tracking a more cryptic prey by selecting to be in that prey species preferred habitat.

Social carnivores are typified by the concept of cooperation among conspecifics, which improves the direct and inclusive fitness of individuals within groups through cooperative hunting, energy acquisition and reproduction of related individuals (Creel and Creel 1995, Van Horn et al. 2004, West et al. 2007, MacNulty et al. 2012). Although cooperation has clear benefits, there are costs associated with cooperation. The overall hunting success of the group increases with additional individuals cooperating in the hunt until the success reaches a plateau (MacNulty et al. 2012). As more individuals cooperate, there is a higher overall energy consumption for the pack as there are more mouths to feed and fewer resources per individual per prey killed (Smith et al. 2008, Sand et al. 2012). Due to the trade-off between cooperating to increase prey capture success and ensuring an individual's own energy acquisition, cooperation in social carnivores may be dynamic and fluctuates depending on prey species available on the landscape. In a large group, a predator may gain more by splitting off and capturing a small prey rather than staying with the group and gaining a small portion of a large prey.

The gray wolf (*Canis lupus*) is a prime example of a social carnivore that relies on cooperative hunting to capture prey often much larger than itself. Although wolves tend

to focus their efforts on capturing large ungulate species (Vucetich et al. 2011, Montgomery et al. 2014, Tallian et al. 2017), they are generalist predators who also capture smaller prey species such as beavers (*Castor canadensis)* and snowshoe hare (*Lepus americanus*) (Fuller and Keith 1980, Gable et al. 2016). Cooperative behaviour is reduced, given the benefit-cost ratio of hunting small prey species (i.e., lower energetic payoff and increased competition between conspecific wolves) (Metz et al. 2011, Sand et al. 2016). Cooperation can be measured through the degree of cohesion within wolf packs, which is known to fluctuate depending on factors such as seasonality and kin-relationships (Barber-Meyer and Mech 2015). Wolves may therefore adjust their level of cohesion to maximize their own energy intake based on prey availability on the landscape. Wolves also use different habitat selection tactics to maximize encounter rates with prey on the landscape (Kittle et al. 2017). Since wolves are generalist predators, they may employ different prey foraging tactics to effectively capture prey, such as targeting areas where prey are more abundant or habitats that are also selected by prey.

Riding Mountain National Park (RMNP - 2,969 km^2; 50°51′50″N 100°02′10″W), located in southwestern Manitoba, Canada, is home to a well-studied wolf population, with studies dating back to the 1970s (Samuel et al. 1978, Carbyn 1983, Paquet 1991), as well as more recently (Sallows 2007, Stronen et al. 2011, 2012). RMNP is primarily composed of aspen parkland, mixed wood forest and boreal forest, interspersed with natural prairie ecosystems (41%, 30%, 7% and 1% of the area respectively). The wolf population has remained relatively stable at around 70 individuals since the early 1990s, with fluctuations due to mortalities associated with outbreaks of canine distemper virus

(CDV) (Stronen et al. 2011). Compared to the surrounding agricultural areas, RMNP represents a stark interface as an island of mostly intact forest-dominated habitat surrounded by agricultural fields. Wolves are protected within RMNP, but farmers and ranchers are permitted to destroy wolves that pose a danger to their cattle outside of the park. The protection afforded by the park coupled with the fact that RMNP has relatively high prey densities (see below), wolves tend to remain in the park, except for occasional forays and dispersal attempts (Stronen et al. 2012).

Similar to other systems in North America, RMNP is a multi-prey system, where wolves prey on elk (*Cervus canadensis*), moose (*Alces alces*), white-tailed deer *Odocoileus virginianus*), and beavers (Sallows 2007). Up until the early 2000s, elk were the most abundant ungulate species and the primary prey species for wolves in RMNP. Historically, RMNP has always been considered a predominantly wolf-elk system. However, due to the Bovine TB (*Mycobacterium bovis*) monitoring program, elk who tested positive for the disease were removed from the population, leading to a decrease in the elk population to the point where moose are currently the more abundant ungulate in RMNP (Parks Canada 2016a). My wolf study was launched in January 2016 to investigate wolf diet in RMNP, which may have changed due to the restructuring of the dominant prey species from elk to moose. Wolves radio-collared during our study demonstrated a high degree of "fission-fusion" within packs, where individuals were not always together, but often made forays in smaller groups or alone. This makes RMNP an ideal system to study how wolves adjust their spatial and social environments to

maximize their energy intake in a system where prey differ in body size, distribution and anti-predator traits.

The integration of these different aspects of hunting behaviour in wolves, i.e., spatial prey foraging tactics and social cohesion, helps paint a clear picture of how wolves adjust their spatial and social environments to maximize their energy intake. Where wolves are located, and whether they are with or without conspecifics may largely depend on the prey species that are present in their environment and on the prey targeted at that time. RMNP is home to an insular yet dynamic wildlife population, where high abundances of species interact in a relatively small area. Understanding how this top predator adjusts its spatial-social environment within the confines of the park will inform management in the event of further changes in prey populations. This work may highlight important landscape characteristics (e.g., habitats or rugged landscapes) based on species distribution that are used by predators. These landscape characteristics could be identified by conservationists and resource managers to promote healthy predator populations which in turn regulate ecosystems. Changes may not only affect where wolves are found in the park, but also their pack dynamics, such as pack size and structure. These attributes relate back to the functional response between predator and prey and are important baselines for monitoring the health and sustainability of an ecosystem.

1.2 Thesis Overview

In my thesis, I attempt to quantify how gray wolf spatial and social environments are shaped by prey distribution in RMNP, a protected natural environment.

In Chapter 2, I test three different hypotheses related to how wolves track two similarly sized but differently spatially distributed prey species on the landscape (i.e., elk and moose); the prey abundance hypothesis, the prey habitat hypothesis and the prey catchability hypothesis. To test these hypotheses, I integrated prey resource selection functions (RSF), prey density and prey vulnerability RSFs into different wolf RSFs to determine which prey variables best explained wolf space use patterns.

In Chapter 3, I tested the hypothesis that energy acquisition mediates sociality in wolves through the trade-off between kill success and resource partitioning where wolves were more cohesive when more likely to encounter large prey and less cohesive when more likely to encounter small prey. To test this hypothesis, I created RSFs for four different prey species found in RMNP (moose, elk, white-tailed deer and beaver). I subsequently tested the effect of these RSF values on the likelihood the GPS collared wolves would be found with other collared pack mates. Furthermore, I tested the effect of these prey RSFs only at locations where wolves had made a kill. Finally, I looked at the influence of prey size on the likelihood of GPS collared wolves being with other collared pack mates at kill sites and scavenging sites.

In Chapter 4, I discuss the implications of my findings for predator-multi-prey systems in general and more specifically RMNP. I further discuss how my results coincide with previous research conducted in the same system and how the shift in prey populations may have implications for the strategies employed by apex predators in multi-prey systems.

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1.3 Co-Authorship Statement

Chapters 2 and 3 of this thesis were a co-authored with Christina M. Prokopenko and Dr. Eric Vander Wal. I was the principal contributor to the data collection, design, data analyses and writing for both chapters. Christina M. Prokopenko contributed to the data collection and gave feedback and support in terms of the analyses and manuscript writing. Dr. Eric Vander Wal contributed to the design and also gave feedback and support in terms of the analyses and manuscript writing. Both chapters will be submitted to peer reviewed journals for publication post thesis completion and will have Christina M. Prokopenko and Dr. Eric Vander Wal as co-authors.

CHAPTER 2: GRAY WOLVES (CANIS LUPUS) FOLLOW THE PREY HABITAT AND PREY CATCHABILITY HYPOTHESES IN A MULTI-PREY SYSTEM

2.1 Abstract

Predators have multiple means by which they can track the distribution of their prey on the landscape. These alternative tactics are described by the prey abundance hypothesis for prey that are aggregated in space, the prey habitat hypothesis for uniformly distributed prey, or the prey catchability hypothesis for prey that are more difficult to capture. The gray wolf (*Canis lupus*), a generalist predator, likely employs multiple tactics when diverse prey with distinct distributions and behaviour are available. I conducted a study on 9 GPS collared wolves in three packs in Riding Mountain National Park, Manitoba, where wolves prey on moose (*Alces alces*) and elk *(Cervus canadensis*). I evaluated wolf selection for prey density, habitat selection and vulnerability on the landscape through Resource Selection Analysis. Wolves selected for moose and elk vulnerability, and moose habitat selection, supporting the prey catchability and prey habitat hypotheses. Surprisingly, wolves avoided moose and elk density, which is counter-intuitive since predators should be selecting area where their prey is more abundant. This density avoidance highlights the ongoing arms race between predator and prey since the negative relationship is most likely due to the prey avoiding the predator. Therefore, wolf space-use is driven by the resources of their primary prey, thereby increasing encounters, and areas on the landscape that improve attack success of their large bodied prey. This work illustrates the role landscape variation plays in predator-prey dynamics.

2.2 Introduction

External factors such as habitat structure and resource distribution shape animals' space use (Johnson et al. 2002, Bjørneraas et al. 2011, Fagan et al. 2013). For example, individuals may differ in movement patterns due to changes in resource availability (Roshier et al. 2008). In the context of a mobile consumer preying on a fixed resource, the consumer selects areas associated with increased resource availability (Jung et al. 2009, Street et al. 2015). In cases where mobile consumers prey on mobile resources, both affect each other's space use. Specifically, predators may use space such that it maximizes their access to prey (Kittle et al. 2015, 2017), whereas prey may adjust their behaviour to avoid predation (Mitchell and Lima 2002, Creel et al. 2005, Kittle et al. 2008). Various hypotheses have been proposed to explain how predators track their prey, leading to encounters, and successful kills. Following functional response and ideal gas law theory, encounter rates between predators and prey increase with increasing prey density (Holling 1959). Predators can exploit this empirical relationship by selecting for areas of higher abundance, where prey are more aggregated, i.e., the prey abundance hypothesis (Weckel et al. 2006). Conversely, where prey are more evenly distributed on the landscape (areas of high abundance are harder to find) the successful tactic would be to select higher quality prey habitat to increase the probability of encounter, i.e., the prey habitat hypothesis (Williams and Flaxman 2012, Latham et al. 2013). Further, post encounter, predators could use a tactic where they select areas in which prey are more vulnerable to predation (Hebblewhite et al. 2005, Petrunenko et al. 2015), i.e., the prey catchability hypothesis (Davidson et al. 2012). Evidence for each of these hypotheses

may be present in a multi-prey system since predators may use one or more of the resulting tactics in concert, as there are multiple unilateral predator-prey relationships in the system (Kittle et al. 2017).

Complexity in the influence of prey abundance increases when there are multiple prey species in a system. The restructuring of prey species abundances in these systems leads to changes in predator diets as predators often respond by making the primary prey the one that is the most abundant on the landscape (primary prey being the prey making up the largest proportion of the diet). (Sillero-Zubiri and Gottelli 1995, Weckel et al. 2006, Garrott et al. 2007). Prey abundance is an essential component of the functional response formulation in predator-prey dynamics where the increase in the number of available prey items lead to higher kill rates (Dale et al. 1994, Zimmermann et al. 2015), likely due to higher encounter rates. The influence of prey abundance on predator-prey dynamics is often assessed in single prey species systems. In terms of space use, predators typically have a non-linear relationship with prey abundance in multi-prey systems. Predators select for areas of high prey abundance when prey abundance reaches a threshold where encounters with prey are more consistent (Kittle et al. 2017). This abundance threshold may be influenced by the degree of aggregation of the prey (Huggard 1993). Random encounters between predator and prey decrease with decreasing prey abundance (Travis and Palmer 2005). Therefore, when prey are neither aggregated nor abundant, predators may use alternative space use strategies that respond to prey density.

When large groups of prey are absent, predators need to rely on other cues to track smaller cryptic groups of prey. Alternative means of tracking prey can be explained by the prey habitat hypothesis. This hypothesis stipulates that predators select habitats preferred by their prey instead of relying on abundance. Adhering to the prey habitat hypothesis should increase the likelihood predators encounter prey when prey abundance is low. Evidence in support of the prey habitat hypothesis is seen in large mammalian predators that select for habitat types preferred by their prey species. For example, wolves selected for forest types that were considered high quality moose habitat (Lesmerises et al. 2012, Kittle et al. 2017). Selecting for high quality prey habitat may be an outcome of remembering where prey species were previously encountered (Janson 1998, Regular et al. 2013). Therefore, it may be advantageous for predators to track prey using the prey habitat tactic when prey are less locally abundant and aggregated in space.

In the context of a multi-prey system, tracking resources through prey abundance and prey habitat quality may be simultaneously adopted by predators in response to differences in prey populations within the system. Species that aggregate in space (Hammond et al. 2007) may elicit the prey abundance tactic, but species that are evenly distributed in space may lead predators to adopt the prey habitat tactic to maximize encounter rates. Generalist predators that target multiple prey species could simultaneously use different tactics. To this effect, few empirical studies have been conducted to test if multiple tactics could be simultaneously employed by a predator in a multi-prey system to increase encounter rates with different prey species (but see Kittle et al. 2017).

The presence of prey on the landscape is not necessarily equivalent to prey being accessible to predators. Prey species can select for habitats that reduce their vulnerability to predators (Stein and Magnuson 1976, Rachlow and Bowyer 1998, Thaker et al. 2011), creating a landscape where prey catchability will vary depending on the underlying habitat features. Another alternative prey foraging hypothesis, the prey catchability hypothesis, therefore posits that predators will select habitats where prey are more vulnerable to predation (Davidson et al. 2012). Habitat where prey are less accessible to predators may be characterized by decreased visibility of prey (Balme et al. 2007) or more opportunities for prey to evade predators (Creel et al. 2005, Hebblewhite et al. 2005, Mao et al. 2005). Hunting in such habitats is energetically more costly due to increased efforts to subdue prey and fewer successful captures (Andruskiw et al. 2008). The importance of using the prey vulnerability tactic may be amplified when there is an increased risk of injury or death for the predator during a predator-prey encounter (Mukherjee and Heithaus 2013). As a result, areas that are more frequently used by prey may be less valuable to predators if the prey are invulnerable to predation. Conversely, prey can be more vulnerable to predation based on habitat type or distance to features such as roads or transition zones between habitats (Grant et al. 2005, Bergman et al. 2006). The prey catchability hypothesis may, therefore, also explain predator space use driven by prey vulnerability on the landscape (Grant et al. 2005).

Gray wolves (*Canis lupus*) are a generalist apex predator that employ a range of tactics to hunt in multi-prey systems; systems that often include prey species ranging from large ungulates to small rodents (Paquet 1992, Mech 1995, Vucetich et al. 2011).

Although wolves prey on multiple species within a system, they usually have a primary prey species that can change based on different factors. Prey switching is typically thought to be driven by species prey density (Sand et al. 2016, Tallian et al. 2017). This highlights the direct influence of prey abundance on hunting tactics of wolves in multi-prey systems; however, the tactics adopted may rely on density, habitat quality, or vulnerability of prey at finer spatial extents. Although wolves may have primary prey species that make up the largest portion in their diet in a system, they still frequently capture alternative prey species (Huggard 1993, Metz et al. 2012). The consumption of multiple prey suggests predators may use simultaneous tactics (as articulated by the prey abundance hypothesis, the prey habitat hypothesis, and prey catchability hypothesis) which represents a bet-hedging strategy in multi-prey systems.

Here I test the aforementioned three prey foraging hypotheses in a multi-prey system: prey abundance hypothesis, prey habitat hypothesis, and prey catchability hypothesis. Wolves prey on elk (*Cervus canadensis*) and moose (*Alces alces*) in Riding Mountain National Park (RMNP). Elk are more social than moose, and are found aggregated in larger groups (Altmann 1959, Vander Wal et al. 2013). Wolves should adjust space use to maximize encounter rates with both ungulate species based on the fine scale abundance of both moose and elk. I compared wolf spatial selection to density, habitat selection, and vulnerability of moose and elk on the landscape to test the three hypotheses. Based on the prey abundance hypothesis, I predicted that wolves will select for areas of high density of prey species that live in more aggregated groups on the landscape, i.e., elk (P1). In contrast, based on the prey habitat hypothesis, wolves will

select for areas of high habitat quality for prey species (measured using resource selection functions) who are relatively less dense but more evenly distributed on the landscape, i.e., moose (Figure 2.1) (P2). Finally, for the prey catchability hypothesis, I predicted that wolves will select more strongly for vulnerability on the landscape for prey species that are more dangerous to capture, i.e., moose (P3). Understanding the tactics used by predators relative to the distribution of multiple prey species on the landscape will help understand predator-prey relationships that may be present in a multi-prey system.

2.3 Methods

2.3.1 Study site and species

Riding Mountain National Park (RMNP) is an insular protected area surrounded by agriculture (2,969 km^2; 50°51′50″N 100°02′10″W). RMNP is primarily composed of aspen parkland and boreal forests, dominated by tree species such as trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banskiana*). Wolves are the apex predator in this system followed by black bears (*Ursus americanus*). The wolf population in 2016 was estimated at 72 individuals (Parks Canada 2017). Prey species of wolves have been historically abundant in RMNP (Carbyn 1980); these species include elk, moose, white-tailed deer (*Odocoileus virginianus*) and beavers (*Castor canadensis*). Although ungulate numbers have decreased in more recent years, their abundance is still relatively high (Parks Canada 2016a). Elk and moose have historically been, and still are, the two main prey species for wolves in the park (Sallows 2007) with their populations estimated at 1,200 and 2,900 individuals respectively in 2016 (Vander Wal et al. 2013, van Beest et al. 2014, Parks

Canada 2016a). White-tailed deer are less abundant within the park with their population estimated at around 900 individuals and are primarily located near the townsites and park boundary (Parks Canada 2016a). For this reason, and the few white-tailed deer kills found during this study in 2016 (n = 1 or 4% of all kills), white-tailed deer were excluded from the analysis.

2.3.2 Analysis overview

I sought to test the influence of three prey distribution metrics (density, habitat selection, and habitat-based vulnerability) on space use of wolves fitted with GPS collars. I used a combination of visual aerial survey observations of elk and moose, and biotelemetry data from GPS collared elk to calculate density and prey habitat selection. I calculated prey vulnerability by using wolf kill sites identified from wolf biotelemetry data (see Figure 2.2 for analysis overview).

2.3.3 Data

2.3.3.1 GPS-collar data

Wolves (n = 9) from three packs in the western portion of RMNP were fitted with GPS collars in Jan-Feb 2016. A map of the pack home ranges can be found in Appendix A (Figure A1). Bighorn Helicopters Inc, contracted through Parks Canada, captured the wolves using nets launched from a helicopter (Memorial University AUP 16-02-EV). Collars collected GPS fixes every 2 hours (e.g. four taking locations on even numbered hours and five on odd numbered hours).

I used GPS data from collared elk (n = 19) to create a winter habitat selection model. Elk were captured in January 2016 using aerial captures (Memorial University

AUP 16-02-EV) and fitted with GPS collars that dropped off in December 2016. Collars recorded GPS fixes every two hours for each elk and relocations from January – April 2016 were retained for this study. Locations found outside of the park boundary were excluded (n = 4,384) resulting in a total of n = 16,617 relocations.

2.3.3.2 Ungulate aerial survey data

I used visual observations of moose and elk to quantify prey abundance and habitat selection from the annual ungulate survey conducted by Parks Canada in February 2016. Parks Canada conducts an annual ungulate survey using a helicopter (Parks Canada 2016a) where observers on either side of the aircraft counted moose and elk within 200m of the aircraft and recorded the spatial location of observed individuals and group size. The survey transects are flown north–south at intervals of approximately 400m spanning the territories of collared wolves (western RMNP, Appendix A; Figure A2).

2.3.4 Analysis

I tested the influence of three different prey metrics: density, habitat selection, and vulnerability on wolf resource selection using a resource selection function (RSF) framework. RSFs are models that determine the probability of space use measured at the level of individuals, populations, or species by comparing used vs. available resource units (McLoughlin et al. 2010, Boyce et al. 2015).

2.3.4.1 Prey Density

To measure prey density for moose and elk, I converted visual observations from the 100% coverage ungulate survey into quantifiable density by partitioning the area covered by the survey into a 400m x 400m grid using the Create Fishnet tool from ArcGIS 10.3.1

(ESRI 2016). Although this data is a snapshot in time of the distribution of moose and elk densities, the values are representative of the general distribution of moose and elk winter densities in RMNP. This is made evident by the correlation between the 2016 density data and the mean densities from 2015 to 2017 (Appendix B; Figure B1). I calculated density for moose and elk by dividing the number of individuals observed in each cell by the area of the corresponding cell.

2.3.4.2 Prey Habitat Selection

I used the survey data for moose and GPS-collar data for elk to construct RSFs to determine their habitat selection on the landscape using land cover classes and distances to features as explanatory variables in the models (Appendix C; Table C1).

I used georeferenced visual observations from the 100% coverage ungulate survey (Appendix A; Figure A2) conducted by Parks Canada to gather locations for the moose RSF (for an example, see van Beest et al. 2014). I classified each moose observation as a used point in the RSF model (van Beest et al. 2014, Street et al. 2015). A uniform distribution of points was generated every 600 m along the transect lines to model available points for the RSF (Street et al. 2015). Whereas for elk, I identified winter home ranges by generating 100% minimum convex polygons around each individuals' relocations from January – April using Home Range Tools for ArcGIS (Rodgers et al. 2015). I used a uniform sampling method, by generating regular grids of points (90m × 90m) to simulate available points within home ranges for each individual. This uniform sampling method better covered the entirety of the available landscape compared to randomly generated points. This sampling approach is a common alternative to random

sampling and has been found to reduce bias (Warton and Shepherd 2010, Aarts et al. 2012, Benson 2013, Renner et al. 2015, Prokopenko et al. 2017).

I selected the final set of covariates by comparing sets of *a priori* models for moose and elk separately using Akaike's Information Criterion (AIC) (Appendix C; Table C1) and checked for potential correlation between covariates in the final model (Appendix C; Figure C1). Covariates included in the final model for both moose and elk were: proportion of land cover type (Manitoba Remote Sensing Centre 2004) within 500m (i.e., grassland, mixed wood forest, marsh, bog, coniferous forest and open deciduous forest), distance to water, distance to streams, and terrain ruggedness. In addition, the moose model included distances to paved and unpaved roads while the elk model included distance to maintained trails and unmaintained backcountry trails (Latham et al. 2013, van Beest et al. 2014). Distances were included in the model as natural logarithm transformed distance +1 to account for the decay in animal response to proximity to features (Prokopenko et al. 2017). Terrain ruggedness was calculated using the Terrain function found in the R package "raster" (Hijmans et al. 2017). Animal ID was included in the elk model as a random factor to control for variation between individuals (Gillies et al. 2006).

2.3.4.3 Prey Vulnerability

To model prey vulnerability on the landscape, I used data collected from kill site investigations conducted on the three collared packs during the winter of 2016 (January – April 2016). Clustered GPS points were used to identify possible wolf kill sites for each pack and were visited on the ground to confirm the presence of a kill site (Webb et al.

2008). A total of n = 1,614 clusters were identified using an algorithm used to locate potential wolf kill sites using GPS relocations (Warren 2008). Parameters used to determine a cluster consisted of a maximum of 300 meters between two relocations within 96 hours (the algorithm can be provided upon request). Out of the clusters identified, n = 564 were investigated. Sites were visited along a random stratified sampling procedure where I attempted to visit the same amount of large and small clusters. Most sites were easily accessible via snowmobile, but a helicopter was used on multiple occasions for sites that were not accessible on foot or by snowmobile. Based on the investigations, I located n = 32 moose and n = 11 elk kill sites.

I used kill sites as 'used' locations on the landscape and determined home ranges for corresponding wolf packs by generating 100% minimum convex polygons using Home Range Tools for ArcGIS (Rodgers et al. 2015) to create kill site RSFs. I used the MCPs to determine the extent of available habitat on the landscape by generating uniform grids of points (600m × 600m) to simulate available points within each pack's home range (Warton and Shepherd 2010, Aarts et al. 2012, Renner et al. 2015, Prokopenko et al. 2017).

The top model describing moose and elk vulnerability to wolf predation was selected by comparing *a priori* models for moose and elk using AIC (Appendix C; Table C1). Covariates in both the final moose and elk vulnerability were: proportion of land cover type (Manitoba Remote Sensing Centre 2004) within 500m (i.e., grassland, mixed wood forest, bog, coniferous forest, and open deciduous forest). In addition, proportion of marsh land cover type and distance to stream were included in the moose vulnerability

model while distance to hard edge (Bergman et al. 2006) and terrain ruggedness were included in the elk vulnerability model. Hard edge consisted of transition zones between open cover and closed cover habitats and has been documented to influence prey vulnerability on the landscape (Bergman et al. 2006). Pack ID was included in the model as a random factor to control for variation between packs (Dickie et al. 2017).

2.3.4.4 Wolf RSF

I used GPS data from the 9 collared wolves to create the RSF framework to test the influence of prey density, prey habitat and prey vulnerability. GPS points located outside of the park and outside of the area covered by the 100% coverage ungulate survey (Appendix A; Figure A1) were excluded from the analysis (n = 1,098), giving a total of n = 3,226 used points. Home ranges for individual wolves were identified by generating 100% minimum convex polygons using Home Range Tools for ArcGIS (Rodgers et al. 2015) and portions outside of the park and the area covered by the 100% coverage ungulate survey were removed due to the stark change in habitat outside of the park and the lack of prey abundance measurements outside of the 100% coverage ungulate survey area. I generated uniform grids of points (150m × 150m) to quantify habitat and prey distribution within the home ranges of each individual. This uniform sampling method better covered the entirety of the available landscape compared to randomly generated points (Warton and Shepherd 2010, Aarts et al. 2012, Renner et al. 2015, Prokopenko et al. 2017).

I compared six *a priori* models to determine the habitat and landscape covariates to include into the wolf habitat model (Appendix C; Table C1). The final covariates

included the proportion of land cover type in a 500m buffer (i.e., grassland, mixed forest, marsh, bog, coniferous forest, and open deciduous forest), distance to water, distance to stream, distance to hard edge (Bergman et al. 2006) and terrain ruggedness (Hijmans et al. 2017). Pack and individual ID were included in the model as random factors (Gillies et al. 2006).

I tested the effect of prey density, prey habitat selection and prey vulnerability on wolf resource selection using thirteen *a priori* generalized linear mixed models with a binomial distribution using the R package lme4, including models with interactions (Bates et al. 2015). The thirteen models were selected to determine which combinations of prey density, prey habitat selection and prey vulnerability best explained wolf resource selection. I included the covariates from the wolf habitat RSF to tease apart the effects of habitat and prey distribution on wolf resource selection (Table 2.1). I ensured that there was no correlation between prey distribution covariates (Appendix C; Figure C1). I evaluated the best grain at which to measure each prey distribution covariate by comparing AIC values of models containing the mean value of each covariate within 30m, 100m, 250m, 500m, 1000m, 2000m and 4000m buffers (Laforge et al. 2015). The best grain was selected by retaining the extent with the lowest AIC score (Appendix C; Table C2). The top model was selected using AIC (Table 2.1). I tested the final model for multicollinearity issues and subsequently removed distance to stream from the final model as it was correlated with moose vulnerability. The final model was cross validated using a three fold k-fold cross validation test (Roberts et al. 2017) where each pack was treated as spatially independent since their home ranges did not overlap.

2.4 Results

All three prey distribution metrics influenced wolf space use. The best supported model describing space use by wolves included both prey habitat selection and density as well as moose vulnerability. An interaction between moose habitat selection and moose vulnerability was also included in the best supported model (conditional $R^2 = 0.14$, mean K-fold = 0.91; see Table 2.1).

2.4.1 Prey density, Prey habitat selection and Prey vulnerability

Elk density values within the 400m x 400m cells in wolf territories ranged from 0 to 168.5 individuals / km^2 and moose from 0 to 37.5 individuals / km^2 in the 400m × 400m cells. Within cells that had at least one observed moose or elk respectively, mean elk density was 27.16 individuals / km^2 (SD = 36.52) while mean moose density was 10.56 individuals / km^2 (SD = 5.73) (Figure 2.1). These results highlighted that in general elk are more aggregated and found in larger groups relative to moose. Moose were consistently found in smaller groups as shown by the small variance and lower average density in the cells. Moose avoided bogs, coniferous forests, open deciduous forests, open water, unpaved roads and rugged terrain (Appendix C; Table C3). Elk selected for unmaintained trails and avoided grasslands, mixed wood forests, marshes, bogs, open deciduous forests, open water, streams and maintained trails (Appendix C; Table C3). Moose were killed closer to streams while elk were killed in more rugged terrain and closer to hard habitat edges (Appendix C; Table C3).

2.4.2 Wolf RSF

Wolves avoided grasslands (β = -3.58; 95% CI = [-4.63; -2.52), mixed wood forests (β = -0.40; 95% CI = [-0.72; -0.08]), and bogs (β = -1.19; 95% CI = [-2.15; -0.24]). Wolves selected for coniferous forests (β = 5.73; 95% CI = [4.51; 6.96]), hard edges between habitats (β = -0.90; 95% CI = [-1.05; -0.74]), and terrain ruggedness (β = 7.45; 95% CI = [6.45; 8.45]) (Table 2.2).

For the prey distribution variables, the top model with the lowest AIC score contained all prey distribution measures for both species except for elk vulnerability. The top model also contained an interaction between moose habitat selection and moose vulnerability (Table 2.2). Wolves selected for areas where moose habitat selection was high (β = 0.40; 95% CI = [0.05; 0.75]) and moose vulnerability was high (β = 2.17; 95% CI = [0.53; 3.80]); note, however, the differences in effect size. Wolves also significantly selected for the interaction of these two variables, areas where both moose habitat selection and moose vulnerability were high (β = 6.45; 95% CI = [4.05; 8.85]) (Table 2.2). In addition, elk habitat selection was significantly selected for (β = 0.32; 95% CI = [0.01; 0.63]), although to a lesser extent than moose habitat selection (Table 2.2). Wolves avoided areas of higher moose and elk density (β = -2.89; 95% CI = [-3.33; -2.46] and β = -1.87; 95% CI = [-3.52; -0.21] respectively; see Table 2.2). The influence of prey densities on wolf space use did not differ significantly between the two prey species (Figure 2.3).

2.5 Discussion

In this chapter of my thesis, I tested three hypotheses that described predator space use in a multi-prey system. The k-fold test performed on the final wolf RSF demonstrates the robustness of the model and gives confidence in the underlying prey models. Prior k-fold validations using the method proposed by Boyce et al. (2002) were conducted on models using similar aerial survey data from RMNP with confident results (van Beest et al. 2014). As I predicted, wolves selected for the habitat of prey that were more evenly distributed on the landscape, i.e. moose, thus supporting the prey habitat hypothesis. However, I did not find support for the prey abundance hypothesis for either moose or elk. The prey abundance hypothesis predicts wolves would select for prey density of the prey species that was more aggregated on the landscape, i.e., elk. Instead, wolves appear to select elk habitat quality instead of elk density. Further, in agreement with the prey catchability hypothesis, wolves appeared to select for moose vulnerability on the landscape. These hypotheses were not mutually exclusive, specifically, wolves appeared to increase their chances of encountering and subduing prey by using areas where moose are simultaneously predictable and vulnerable. I failed to detect a similar effect for wolf-elk interactions; while wolves selected for elk habitat selection, there was no evidence they selected for elk vulnerability.

Predators should work to increase their encounter rates and capture success to maximize their energetic gain from prey. In multi-prey systems, the optimal tactic to use when hunting dissimilar prey will differ based on prey traits such as distribution and behaviour, thus the predator is faced with resolving the conflict between these divergent

behaviours. For example, wolves used the prey habitat tactic for moose, as expected, but surprisingly for elk as well, counter to my predictions. Previous studies have also demonstrated wolf selection for habitat types preferred by prey (Lesmerises et al. 2012, Kittle et al. 2017); and in some instances found evidence that wolves selected directly for the probability of prey habitat selection (Roffler et al. 2018). This phenomenon of selecting for prey habitat is seen in a broad range of taxa; seven-spotted lady beetles (*Coccinella septempunctata*) selected for higher quality patches for their prey even in the absence of prey (Williams and Flaxman 2012). Selecting for prey habitat may be linked to attribute memory (remembering habitat types where they had encountered prey before) to inform subsequent decisions (Kamil and Roitblat 1985). Selection for elk habitat may come as a result of wolves focusing their hunting on elk that are solitary or in smaller groups. Using a prey foraging tactic that is optimal for one prey species and then also using it for a subset of another prey species may be more beneficial for the predator rather than trying to implement two different tactics simultaneously.

Although predators may successfully encounter a prey species, be it through prey abundance or habitat, they may not be able to capture it. Prey vulnerability has been shown to be an important factor in predator space use (Messier and Barrette 1985, Patterson and Messier 2001, Grant et al. 2005, Balme et al. 2007, Petrunenko et al. 2015). Ungulates are known to injure or kill wolves in confrontations (Mukherjee and Heithaus 2013) and so as predicted, wolf space use was best defined by the vulnerability of their larger and more dangerous prey species, i.e., moose. Wolves selected for moose vulnerability more so than for moose habitat quality, suggesting the prey catchability

tactic was the main driver used by wolves in RMNP, consisting of frequenting areas with habitat characteristics similar to locations where they had made successful kills. Moose are large and are known to be more likely to survive encounters with wolves if they stand their ground (Sand et al. 2016), leading wolves to probably rely more on the landscape to facilitate the capture of moose. Elk instead rely on group size to dilute risk (Hebblewhite and Pletscher 2002), which may explain the lack of observed response by wolves selecting for elk density or vulnerability, if wolves are indeed targeting more segregated elk using the prey habitat tactic. This seems to suggest that the benefits of being able to capture prey when encountered outweigh the benefits of encountering prey more often.

My work suggests that moose are targeted as the primary prey in RMNP, given the larger effect size for moose habitat on wolf space use relative to elk (1.24:1) in addition to selecting strongly for moose vulnerability. These results suggest that wolves in RMNP may be using two different tactics in conjunction to effectively track their primary prey, first, to increase their likelihood of encountering the prey and second to increase the likelihood of capturing the prey. During my thesis in RMNP, the moose population is larger than that of the elk population (Parks Canada 2016a). In multi-prey systems, predators often have a primary or preferred prey that is defined by its abundance and vulnerability. For example, wolves relied on elk as their primary prey in Yellowstone National Park, USA, and maintained their preference for elk even with an increase in the bison (*Bison bison*) population (Tallian et al. 2017). This was not the case in RMNP, where moose were more abundant relative to elk during my study (2.45:1) (Parks Canada 2016a) and kill-sites demonstrate that moose were the primary prey species for wolves at

that time (2.91:1). Historically, elk surpassed moose in abundance in RMNP, and elk were the primary prey species for wolves (Carbyn 1983). Thus, with the change in prey abundance, wolves now seem to prioritize tracking moose while simultaneously tracking elk, to maximize kill success. Wolves preyed very little on white-tailed deer in RMNP during the study period (Appendix C; Figure C2) possibly due to their lower overall numbers or their spatial distribution concentrated towards the park boundary. In another multi-prey system, Kittle et al. (2017) found wolves selected for moose distribution and not that of caribou (*Rangifer tarandus*), possibly due to the much larger gap between these prey species abundance in that study area. The abundance of moose and elk in RMNP were much closer, making the prospect of targeting multiple prey more profitable.

The lack of selection of elk density by wolves may be due to low elk numbers in RMNP. A previous study demonstrated that wolves encountered larger elk herds more frequently than expected based on their availability (Hebblewhite and Pletscher 2002); however, the majority of the elk (58%) in that study were in herds of ≥ 30 individuals, which is typically larger than herds found in RMNP (Vander Wal et al. 2013). Elk use two different strategies to avoid predation; either by being in small groups to avoid detection or in larger groups to dilute individual risk (Hebblewhite and Pletscher 2002). Elk may be using the former tactic due to their overall lower numbers in RMNP, creating smaller aggregations below the threshold necessary to make the prey abundance tactic viable (Huggard 1993). This current lower abundance of elk may be leading wolves to select elk in the same way they do moose, since elk are no longer in large easily detectable herds.

Prey density and prey habitat are sometimes interconnected and simultaneously exploited by predators (Castillo et al. 2013). However, there can also be a disconnect between prey density and prey habitat selection that may be explained by the "leap-frogging" hypothesis (Sih 2005), where prey select lower quality resources to avoid predation and therefore trade-off the benefits of high quality resources to reduce predation risks (Lima and Dill 1990, Heithaus and Dill 2006). An experimental study of dragonflies (*Aeshna palmata*) and their prey showed that predator presence reduced the influence of resource distribution on prey movement, suggesting that prey trade-off the benefits from resources with the costs of predation (Hammond et al. 2007). Predators then have a wider array of habitats to cover to track prey, which reduces search efficiency and increases prey fitness. Other studies have demonstrated that wolves respond similarly to prey by selecting for habitat types best preferred by the prey species, in addition to selecting for prey density at sites where prey density was higher (Kittle et al. 2017). Predators may employ additional strategies such as using linear features to increase search efficiency (McKenzie et al. 2012) or focus on areas of prey vulnerability (Grant et al. 2005, Andruskiw et al. 2008) to increase capture probability after an encounter.

The counter-intuitive result of wolves avoiding prey density at the extent of their home range could be driven by fine-scale strategies employed by the prey. Specifically, in this study the observed avoidance of prey density could be due to prey avoiding wolves at a smaller extent. Similar results were found in a multi-prey system involving wolves, moose, and caribou, where wolves seemed to avoid caribou relocations (Kittle et al. 2017). Kittle et al. (2017) also found that wolves selected for greater moose density,

which is a finding counter to my results. They calculated moose density in a similar way by using aerial surveys, however their transects were much sparser (5 km apart) leading to a coarser scale measure of density. Most studies that find a positive relationship between predator space use and prey density do so at a coarser scale. In those studies, predators tend to reduce overall space use, i.e., home range, in response to areas with high prey density (Patterson and Messier 2001, Kittle et al. 2015, Petrunenko et al. 2015), which could decrease costs associated with protecting one's territory. This therefore suggests that predators may select for prey density at the home range extent by adjusting home range size according to available prey abundance (Valeix et al. 2012). At a smaller scale, predators and prey mutually influence each other's space use (Schneider and Piatt 1986, Rose and Leggett 1990, Mitchell and Lima 2002), creating a potential fine scale spatial arms race between wolves and their prey where the former tries to increase the chances of encounter and the latter attempts the opposite. This work further highlights the importance of scale when studying spatial predator-prey relationships, and that predators may be required to use alternate tactics of foraging for prey due to lower overall prey density or active predator avoidance by prey.

My findings support the prey catchability and prey vulnerability hypotheses as the main drivers of wolf space use in RMNP, which is also the main driver in other systems involving large mammalian carnivores (Grant et al. 2005, Balme et al. 2007, Davidson et al. 2012, Kittle et al. 2017). When tracking their primary prey, wolves appear to hedge their bets between encountering and capturing prey by using space that is both predictable moose habitat but also habitat where moose are vulnerable. This increases the

likelihood of encountering, and subsequently capturing prey. Adopting the tactic best suited for their primary prey, wolves in this system also rely on the same tactic to track a secondary prey due to the lack of large elk herds. Prey density at this fine scale seemed to be attributed to prey anti-predator behaviour instead of a viable prey foraging tactic. Here I showed how a predator tracked two prey species that although similar, differed in abundance, habitat selection, and vulnerability. Further work is needed to explore the interactive effects of prey species distributions on predators in cases where prey species may differ greatly in traits such as body size, vulnerability, and temporal availability. Beaver are known to be an important source of food for wolves in the summer (Benson et al. 2015), and it may mean that the tactics employed by wolves in RMNP may shift based on seasonality. The beaver survey did not coincide in time with the moose and elk aerial survey, meaning that I was not able to test the effect of beaver distribution on wolf habitat selection in this multi-prey context. White-tailed deer did not seem to play a major role in wolf diet during this study (Appendix C; Figure C2) due to lower abundances, however if abundances did increase, wolves may shift their attention to this more vulnerable intermediately sized prey species (Sand et al. 2016). As most predator-prey systems are in fact multi-prey, answering these questions helps shed light on the underlying mechanisms that exist between predator and prey habitat selection.

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Table 2.1. Models considering effects of prey habitat selection, density and vulnerability on wolf space use with their respective K, Δ AIC, Δ AIC weight, log likelihood, Marginal R2, conditional R2 and mean k-fold. Data used in the models were from GPS-collared wolves (*n* = 9) from three wolf packs located in Riding Mountain National Park, Manitoba, from January to February 2016. Best model is shown in bold.

Model	Variables	K	Δ AIC	Δ AIC wt	logLik	Marginal R^2	Conditional R^2	K-fold
Model 10	**Habitat + $M_H \times M_V + M_D + E_H + E_D$**	**18**	**0.00**	**1.00**	**-10328.50**	**0.11**	**0.14**	**0.91**
Model 13	Habitat + $M_H + E_H + M_V + M_D \times E_D$	18	18.95	0.00	-10337.98	0.11	0.14	
Model 7	Habitat + $M_H + M_D + M_V + E_H + E_D$	17	25.56	0.00	-10342.28	0.11	0.14	
Model 11	Habitat + $M_H + M_V \times M_D + E_H + E_D$	18	25.61	0.00	-10341.31	0.11	0.14	
Model 9	Habitat + $M_H + M_D + M_V + E_D + E_H + E_V$	18	26.70	0.00	-10341.85	0.11	0.14	
Model 12	Habitat + $M_H \times E_H + M_V + M_D + E_D$	18	27.44	0.00	-10342.22	0.11	0.14	
Model 6	Habitat + $M_H + M_D + E_H + E_D$	16	246.68	0.00	-10453.85	0.10	0.12	
Model 8	Habitat + $M_H + M_D + E_D + E_H + E_V$	17	248.33	0.00	-10453.67	0.10	0.12	
Model 4	Habitat + $M_D + E_H$	14	337.22	0.00	-10501.12	0.09	0.09	
Model 2	Habitat + $M_D + E_D$	14	354.61	0.00	-10509.81	0.09	0.09	
Model 3	Habitat + $M_H + E_H$	14	464.32	0.00	-10564.67	0.08	0.10	
Model 5	Habitat + $M_H + E_D$	14	464.40	0.00	-10564.71	0.07	0.09	
Model 1	Habitat	12	564.59	0.00	-10616.80	0.06	0.06	

M_H = Moose habitat selection
E_H = Elk habitat selection
M_D = Moose density
E_D = Elk density
M_V = Moose vulnerability
E_V = Elk vulnerability

Table 2.2. Coefficients, standard errors and p-values of variables of the top model considering effects of habitat and prey distribution on GPS-collared wolf (n = 9) space use in three wolf packs from January to February 2016 in Riding Mountain National Park, Manitoba. Significant p-values ($p < 0.05$) are shown in bold.

Variable	Coefficient	St. Error	P-value
Intercept	-2.80	0.22	**< 0.001**
Grassland	-3.58	0.54	**< 0.001**
Mixed wood forest	-0.40	0.16	**0.01**
Marsh	-0.24	0.17	0.16
Bog	-1.20	0.49	**0.01**
Coniferous forest	5.74	0.62	**< 0.001**
Open deciduous forest	0.07	0.27	0.80
Distance to water	-0.20	0.12	0.11
Distance to hard edge	-0.90	0.08	**< 0.001**
Terrain ruggedness	7.45	0.51	**< 0.001**
Moose habitat	0.40	0.18	**0.03**
Elk habitat	0.32	0.16	**0.05**
Moose density	-2.89	0.22	**< 0.001**
Elk density	-1.87	0.84	**0.03**
Moose vulnerability	2.17	0.84	**0.01**
Moose habitat × Moose vulnerability	6.45	1.23	**< 0.001**

Figure 2.1. Kernel density estimates for (a) elk and (b) moose abundance based on an aerial survey conducted by Parks Canada in February 2016 in Riding Mountain National Park, Manitoba. Kernel density was calculated using the Kernel Density tool in ArcGIS 10.3.1 (ESRI 2016).

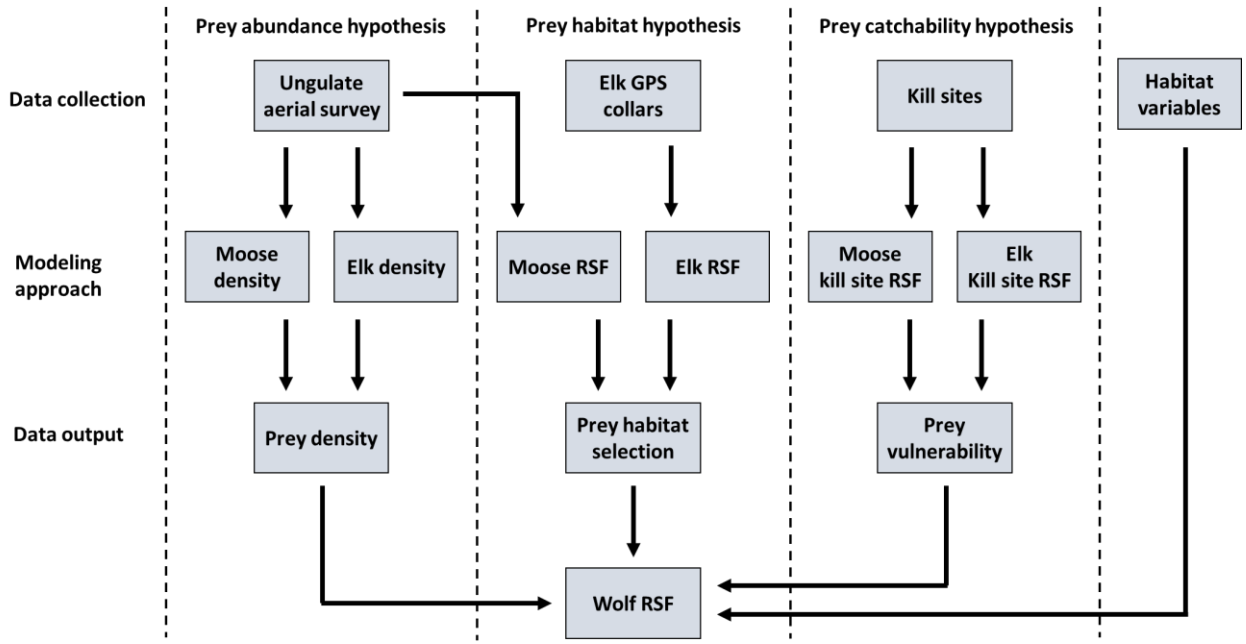

Figure 2.2. Flow chart of methods used to generate the three different prey distribution metrics to test the use of the prey abundance, prey habitat and prey catchability tactics by wolves (n = 9) in three wolf packs in Riding Mountain National Park, Manitoba, from January-February 2016. Columns within dotted lines represent steps to generate the prey distribution metrics for each of the three hypotheses governing the tactics (i.e., prey abundance hypothesis, prey habitat hypothesis and prey catchability hypothesis).

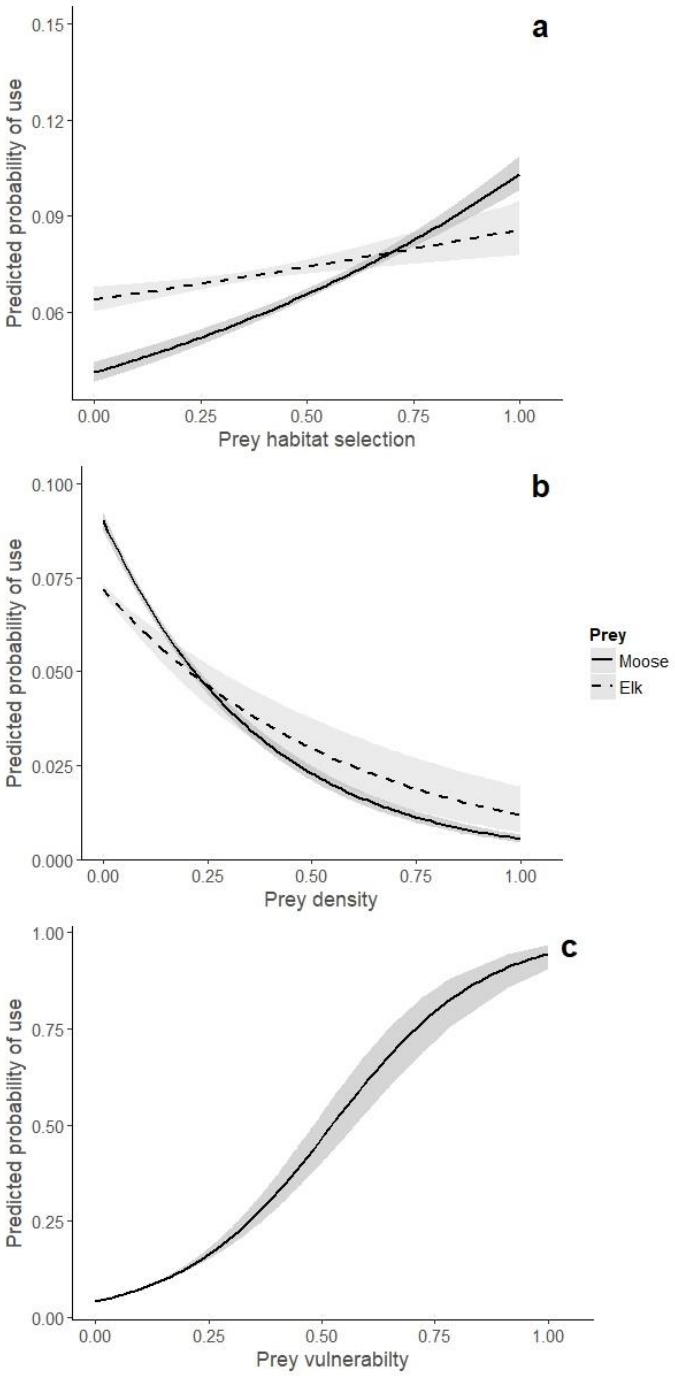

Figure 2.3. Predicted probability of wolf (*n* = 9) space use in three wolf packs in Riding Mountain National Park, Manitoba, Canada from January to February 2016, in relation to moose and elk (a) habitat selection and (b) density, as well as (c) moose vulnerability on

the landscape. All three prey distribution metrics were standardized between 0 and 1 for comparison. Original units for prey density were individuals / km^2 while prey habitat and prey vulnerability did not have units due to being unitless RSF values. Prey vulnerability had the strongest positive affect on wolf space use while prey density was seemingly avoided by wolves. The y-axes are at different scales to allow for better comparison between the effects of moose and elk distribution.

CHAPTER 3: THE EFFECTS OF PREY ON PACK COHESION ON A SOCIAL CARNIVORE, *CANIS LUPUS*, IN A MULTI-PREY SYSTEM

3.1 Abstract

The contrast of costs and benefits seen through cooperation vs. individuality is characteristic in social carnivores. Wolves may trade-off prey acquisition and resource partitioning among conspecifics. For example, individuals can cooperate when attacking larger prey or dissociate to capture smaller prey. Based on this, I hypothesised that energy acquisition mediates sociality in wolves through the trade-off between kill success and resource partitioning. I conducted a study on 12 GPS collared wolves in three packs in Riding Mountain National Park, a multi-prey system where prey vary in body size and seasonal availability. I identified sites as clusters of locations that indicated areas intensely used by individual wolves, including kill sites. Cohesion was determined through temporal and spatial overlap of clusters. I then related cohesion at clusters to species-specific prey availability. I subsequently related cohesion at a subset of clusters confirmed as kills to prey species captured by wolves. I found that cohesion increased with large prey availability (i.e., moose) and decreased with small prey availability (i.e., beaver). However, kill site cohesion was better described by size of prey captured and not prey availability, which could indicate a decoupling between hunting and consuming prey. I tested the link between wolf pack cohesion and prey availability, thus exploring key drivers of pack structure and predator-prey dynamics in systems where wolves may play a regulatory role.

3.2 Introduction

One notable social behaviour is cooperation, which exists in varying contexts in animal societies, varying in purpose (i.e., territory defense, foraging and predator avoidance). Cooperation may be classified as altruistic, with no immediate benefits, or mutualistic, where cooperators receive immediate benefits (Stevens and Hauser 2004). Further, cooperation has been shown to improve the direct and inclusive fitness of individuals within groups through acquisition of resources, survivability and reproduction of related individuals (Creel and Creel 1995, Van Horn et al. 2004, West et al. 2007, MacNulty et al. 2012). However, there are costs to being cooperative, including higher overall energy consumption for the group and fewer resources per individual (Smith et al. 2008, Sand et al. 2012). Cooperation starts to lose to the individuals need when the amount of resources per individual is no longer sustainable. This may occur if the group becomes too large or the prey's energetic value is too small. Increased hunting success is among the most cited explanations for the evolution of social behavior in carnivores (MacDonald 1983). But this belies an important tension typified by optimizing hunting effort for diverse prey with differing vulnerabilities. The degree of cooperation during hunting in social carnivores can be measured through the amount of cohesion between individuals in the group. As such, group cohesion may be dynamic and fluctuate depending on the trade-off between the costs and benefits of cooperation; an idea that has thus far received little attention since social carnivores are often perceived as obligate cooperators.

Cooperation often involves behaviours such as altruism that may not be directly beneficial to the individual exhibiting the behaviour, but may be beneficial through the

inclusive fitness of related individuals (West et al. 2007). More cooperators may mean greater payoffs; for example, an increase in the number of cooperating individuals in meerkats (*Surricata surricata*) lead to more weight gain in pups due to more prey items found through improved foraging outcomes (Clutton-Brock et al. 2001). Understanding the feedback mechanism between cooperation and benefits will further solidify our understanding of how behavioural responses to changing environments may influence fitness outcomes. Social carnivores exemplify cooperation when hunting. An increase in the number of individuals cooperatively hunting resulted in higher prey capture success rate as well as the group's ability in capturing larger and more dangerous prey (Creel and Creel 1995, MacNulty et al. 2012, 2014). In addition, more cooperating individuals decreased chase distances during hunts, which translates into increased efficiency (Creel and Creel 1995). Although cooperation is maintained in social carnivore populations due to benefits, the frequency and degree of cooperation is mediated by the costs attributed to individuals (Packer and Ruttan 1988).

Often animals living in groups are assumed to be socially homogenous units; however, it is important to still consider the individual processes, as they may be key drivers of cohesion within these societies (Clutton-Brock 2009). Tensions exist in cooperative societies between group and individual success, where cooperating individuals incur costs. For example, prey species who undertake cooperative vigilance increase their ability to detect predators when more individuals cooperate (Taraborelli et al. 2012), as well as dilute individual risk (Hebblewhite and Pletscher 2002). Since cooperative vigilance entails that individuals be proximally located, it leads to more

competition for high quality forage between conspecifics. In social carnivores, although increased cooperation increases prey capture success rate, it also reduces the amount of food that each individual is entitled to, as prey has to be partitioned with more conspecifics (Smith et al. 2008, Sand et al. 2012). Therefore, individuals need to constantly weigh the options of cooperating with conspecifics or dissociating from the group to maximise their own energy intake.

Drivers behind a social carnivore's decision to join a group at a given time can be multi-faceted and include social factors, as well as external factors such as resource distribution, i.e. prey (Smith et al. 2008). Resource distribution in terms of predators can be defined as the distribution of their prey on the landscape. Prey availability fluctuates through time and space due to seasonal variations and spatial heterogeneity of landscapes (Metz et al. 2012, van Beest et al. 2013). Social carnivores have to adjust their hunting patterns accordingly to maximize their foraging success (Metz et al. 2012, Kittle et al. 2017). In multi-prey systems, where prey vary in body size and seasonal availability, the strategies to minimize costs of cooperation become increasingly complex. Prey body size translates directly into acquired energy for predators and is therefore key in the cooperation trade-off between partitioning large prey with conspecifics or breaking off to capture small prey on ones own. Large prey are more difficult to subdue (MacNulty et al. 2014) and entail higher risks for the individual, leading predators to capture safer small prey. Hunting small prey, however, results in less energy acquired per successful capture. In addition to energetic implications, small prey may require different hunting strategies, such as ambushing and stealth, and may encourage individuals to dissociate to better

capitalize on those strategies (Gable et al. 2016). The act of attempting to capture prey may result in injury for wolves (Mukherjee and Heithaus 2013), therefore cohesion may be driven by subduing dangerous prey rather than available energy due to prey size. This would result in seeing wolves being cohesive during kills but not scavenging events. Considering the risks of injury and hunt failure with the benefits of energy acquisition, cohesion levels in social carnivores may be dynamic and fluctuate depending on prey size and availability; an idea that has thus far received little attention despite its fundamental role in balancing the costs and benefits of foraging as a social predator.

The gray wolf (*Canis lupus*), is a keystone species and social carnivore that typifies the trade-off between cooperative hunting (pre-kill) versus prey sharing (post-kill consumption). Wolves live in packs mostly comprised of related conspecifics, but do on occasion include unrelated individuals (Lehman et al. 1992). These pack units can be composed of a pair to over a dozen individuals (Paquet and Carbyn 2003). Although packs are often thought of as homogenous social units, cohesion amongst members fluctuates depending on factors such as relatedness, seasonality (Barber-Meyer and Mech 2015) and captured prey size (Metz et al. 2011). Wolves are opportunistic predators and prey upon most ungulate species (Paquet 1992, Mech 1995, Vucetich et al. 2011), as well as beavers (*Castor canadensis*), and other small mammals (Fuller and Keith 1980, Gable et al. 2016). Although prey dynamics fluctuate through time and space, wolves tend to focus their efforts on medium sized ungulates that balance the trade off between risk and reward (Carbyn 1977, Paquet 1992, Tallian et al. 2017). When these species are less available on the landscape, wolves turn their attention to larger ungulates such as moose

(*Alces alces*) (Vucetich et al. 2011, Montgomery et al. 2014). Thus, prey availability in a multi-prey system may play a key role in wolf sociality on the landscape. Alterations to hunting tactics may be required to maintain adequate resource partitioning between pack members based on prey availability. Individuals should therefore make decisions to join or not to join one another on their foraging excursions, creating a fluctuation in cohesion levels at a fine scale.

Here I investigate the effects of prey species availability and captured prey on wolf sociality in a multi-prey system. I hypothesise that energy acquisition mediates sociality in wolves through the trade-off between kill success and resource partitioning. From this hypothesis, I derived three predictions: availability of large prey increases the probability of pack cohesion (P1); availability of smaller prey decreases the probability of pack cohesion (P2); and large captured prey increases probability of pack cohesion at kill sites but not at scavenging sites (P3), leading to more wolves being present at large prey kill sites compared to scavenging sites. Understanding the link between cohesion in social carnivores and prey availability will help determine the role of social behaviours in ecosystem mechanisms such as kill rates.

3.3 Methods

3.3.1 Study site and species

Riding Mountain National Park (RMNP) is an insular protected area surrounded by agriculture and primarily composed of aspen parkland and boreal forest (2,969 km^2; 50°51′50″N 100°02′10″W). The main tree species in RMNP are trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and

jack pine (*Pinus banskiana*). Wolves are the apex predators in this system, alongside black bears (*Ursus americanus*). The wolf population in 2016 was estimated at 72 individuals in 13 packs, with pack sizes in RMNP ranging from 2 to 10 individuals, with a few lone individuals (Parks Canada 2017). Wolf prey species have historically been and still are relatively abundant in RMNP (Carbyn 1980); these species include elk (*Cervus canadensis*), moose, white-tailed deer (*Odocoileus virginianus*) and beavers. In 2016, moose were the most abundant ungulate species in RMNP at approximately 2,900 individuals, followed by elk at approximately 1,200 individuals (Parks Canada 2016a). In many systems, beaver are considered an important source of food for wolves in summer (Benson et al. 2015, Gable et al. 2016). Beaver are found throughout RMNP with an approximate population of 15,100 individuals in 2016 (Parks Canada 2016b). Wolves are also commonly known to prey on white-tailed deer (Paquet and Carbyn 2003), which are also present in RMNP.

3.3.2 Analysis overview

I aimed to test the influence of the availability of four prey species (moose, elk, white-tailed deer, and beaver) on the probability of cohesion of wolves fitted with GPS collars. I used a combination of visual aerial survey observations of moose and beaver, and biotelemetry data from GPS collared elk and white-tailed deer to calculate prey habitat selection, which was used as a proxy for prey availability (see Figure 3.1 for analysis overview).

3.3.3 Data

3.3.3.1 GPS-collar data

Between January 2016 and January 2017, n = 12 Global Positioning System (GPS) Iridium radio collars were deployed on wolves from three packs located in the western portion of RMNP (e.g., three or four wolves per pack were collared; see Figure 3.2). Wolves were immobilized for capture using netguns deployed from a helicopter and fitted with the GPS collars by Bighorn Helicopters Inc (Memorial University AUP 16-02-EV).

I used GPS data from collared elk (n = 19) to create winter and summer resource selection functions (RSF) to model elk availability. Elk were captured in January 2016 using the same technique as wolves, i.e. netguns deployed from a helicopter by Bighorn Helicopters Inc (Memorial University AUP 16-02-EV). Collars were remotely removed from elk via a built-in dropping mechanism from September-December 2016. The two-hour interval GPS fixes were separated into two seasons based on the general presence and absence of snow; winter (November–March) and summer (April–October) for each elk. Relocations outside of the park boundary were excluded (n = 23,149), as I was not able to visit wolf clusters on the ground outside of the park boundary. This resulted in n = 15,885 and n = 17,231 relocations in the summer and winter respectively. Based on all animals in both seasons, there was a total of 19 elk-years. Elk-years consisted of the sampling unit, which was the number of elk collared for a year (e.g., one elk collared for two years or two elk collared for one year both corresponded to 2 elk-years).

I used GPS data from collared white-tailed deer (n = 16; McCance 2014) to create winter and summer RSFs. White-tailed deer were collared from December – March of 2013 using modified custom built Clover Box Traps and aerial captures (for capture and collaring details see McCance 2014). Collars remained on the white-tailed deer until March 2015. In total, I had 32 white-tailed deer-years. The two-hour interval GPS fixes were separated into two seasons; winter (November–March) and summer (April–October) for each individual white-tailed deer. Relocations outside of the park boundary were excluded to conform to the territories of the wolves that were sampled, as sites outside of the park were not visited.

3.3.3.2 Aerial survey data

I used georeferenced visual observations from the annual ungulate aerial survey conducted by Parks Canada in February 2016 to gather locations for the RSF (for an example, see van Beest et al. 2014). Transects were flown north-south at approximately every 400m intervals across the western portion of RMNP (Figure 3.2). Observers on either side of a fixed-winged aircraft recorded the number and location of ungulates observed within 200m of the helicopter (Parks Canada 2016a). This resulted in 100% coverage of that portion of the park. Animal-years to not apply to survey data as no GPS collars were used.

To construct the beaver RSF, I used data from the annual RMNP aerial beaver survey conducted by Parks Canada on 12, 13 October 2016 using two fixed wing aircraft (172 Cessna and Citabria). Surveys were conducted in a block design and consisted of 30 survey blocks, of which the 13 most western blocks were used to create the RSF (Figure

3.2). The other blocks were excluded since the eastern portion of RMNP differs from the study site in terms of habitat, landcover and topography. Each block was comprised of 8 north-south transects measuring 5 km and spaced 600m apart (Parks Canada 2016b). Two observers, seated on either side of the aircraft, recorded observed beaver caches up to 300 m from the aircraft. Caches consist of winter food stockpiles and were characterized as piles of freshly cut branches and leaves in ponds next to beaver lodges.

3.3.3.3 Wolf kill site data

Clustered GPS points from the GPS collared wolves were used to identify possible wolf kill sites for each pack and were visited on the ground to confirm that a wolf kill had occurred (Webb et al. 2008). A total of n = 3,027 individual clusters were identified using an algorithm (Warren 2008), of which n = 859 were investigated. Clusters at the same site were removed to address pseudo-replication. This resulted in a total of n = 310 unique spatial clusters. Of these, n = 81 were determined as kill sites, n = 76 of which were of one of the four main prey species (moose, elk, white-tailed deer, or beaver). The remaining kill sites consisted of n = 2 grouse and n = 3 unidentified ungulate calves. In some instances, I identified clusters as scavenging sites (n = 57) based on evidence on site. Clusters were classified as scavenging sites when: 1) evidence suggested the prey had died on its own (i.e., laying on its side); 2) clusters only consisted of 2-3 relocations for large prey kills; or 3) if clusters appeared at known kill sites that had been visited previously and were therefore classified as kill site revisits (i.e., scavenging sites). When possible, I identified the species, age, sex, and body condition of prey remains found at the kill and scavenging sites.

3.3.4 Analysis

3.3.4.1 Wolf Pack Cohesion

I used a binomial metric of cohesion, defined as instances where wolves were found to be unaccompanied by other pack mates and assumed to be alone (0), or accompanied by other collared packmates (i.e., 'together', 1) (Appendix D). I used location fixes of wolves between January 2016 and January 2017 to determine individual space-use in relation to conspecifics. The same clusters of GPS fixes used to identify kill sites were used for this purpose. The clusters identified sites of important wolf activity in addition to kill and scavenging sites (e.g., resting sites, rendez-vous sites, dens) for each collared wolf separately. I identified a total of n = 3,027 individual clusters (average per individual = 253.17; average per pack = 1012.67) containing n = 19,886 individual fixes using the algorithm. Each cluster was buffered 15m before looking for spatial overlap to account for GPS error around the outer relocations in the cluster circle. Cohesion is defined by spatial and temporal overlap of clusters between wolves in the same pack. The cluster dataset was restricted to instances where at least two collared wolves were present in the pack. I determined a total of n = 1,442 spatially unique areas once individual wolf clusters were merged based on their respective attendance to the site.

3.3.4.2 Prey resource selection functions

I used aerial survey data for moose and beaver; and GPS-collar data for elk and white-tailed deer to construct seasonal (when appropriate, i.e., no winter beaver RSF) RSFs. I used these RSFs to determine species-specific habitat selection using land cover classes and distances to features as explanatory variables in the models. RSFs are models that determine the probability of space use by species measured at the level of individual or population by comparing used vs. available resource units (Boyce and McDonald 1999, McLoughlin et al. 2010, Boyce et al. 2015) following the form: $w(x) = exp^{(\beta_0+\beta_1 X_1+\beta_2 X_2+\cdots+\beta_i X_i)}$, where w(x) is the value of the RSF at location x, β_i is the selection coefficient for the i's habitat and x_i is the proportion of the i's habitat at location x.

By estimating the degree to which a species selects for habitats using RSFs, it is possible to estimate the relative use of areas by species (Boyce and McDonald 1999). Seasons were delineated into two categories based on the presence and absence of snow on the ground; winter from November – April and summer from May – October. The prey RSFs were standardized to range from 0 to 1 by dividing each raster cell by the highest value RSF. I extracted RSF values of each prey species at each site location respective to the appropriate season using the Spatial Analyst tool box in Arc GIS 10.3.1 (ESRI 2016). Data manipulation and analyses were conducted using a combination of ArcGIS 10.3.1 (ESRI 2016) and R version 3.3.1 (R Core Team 2016) (see Appendix D).

I used georeferenced visual observations from the 100% coverage ungulate survey to gather locations for the moose RSF (for an example, see van Beest et al. 2014) and

from the beaver survey to gather locations for the beaver RSF (for an example, see Latham et al. 2013). I classified each moose individual and beaver cache observation as a used point in the RSF model (Latham et al. 2013, van Beest et al. 2014, Street et al. 2015). A uniform distribution of points was generated every 600 m along the transect lines to model available points for both RSFs (Street et al. 2015). Whereas for elk and white-tailed deer, I used GPS relocations as used points. I identified winter and summer home ranges for elk and white-tailed deer by generating 100% minimum convex polygons around each individuals' relocations from November – April and May - October using Home Range Tools for ArcGIS (Rodgers et al. 2015). I used a uniform sampling method, by generating regular grids of points (90 m × 90 m) to simulate available points within home ranges for each individual. This uniform sampling method better covered the entirety of the available landscape compared to randomly generated points. This sampling approach is a common alternative to random sampling and has been found to reduce bias (Warton and Shepherd 2010, Aarts et al. 2012, Benson 2013, Renner et al. 2015, Prokopenko et al. 2017).

I selected the final set of covariates by comparing sets of *a priori* models for moose, elk, white-tailed deer, and beaver separately using Akaike's Information Criterion (AIC; Appendix E; Table E1). Covariates included in the final model for all species were: proportion of land cover type (Manitoba Remote Sensing Centre 2004) within 500 m (i.e., grassland, mixed wood forest, marsh (except beaver), bog, coniferous forest and open deciduous forest) and distance to water. In addition, the moose model included distance to paved and unpaved roads, and terrain ruggedness. The elk and white-tailed

deer models included distance to maintained trails and unmaintained backcountry trails, distance to streams, and terrain ruggedness (Latham et al. 2013, van Beest et al. 2014). The beaver model included distance to marshes in addition to distance to maintained trails and unmaintained backcountry trails. Distances were included in the model as natural logarithm transformed distance +1 to account for the decay in animal response to proximity to features (Prokopenko et al. 2017). Terrain ruggedness was calculated using the Terrain function found in the R package "raster" (Hijmans et al. 2017). Animal ID was included in the elk and white-tailed deer models as a random factor to control for variation between individuals (Gillies et al. 2006) (see Appendix E; Table E2 for the outputs of the final RSF models).

3.3.4.3 Statistical Analyses

I assessed seasonal overlap of wolf cluster locations (i.e., sites) and the calculated RSF values of each prey species to determine the relationship between the number of wolves present at the site and the probability of prey using that space. The location of the site used was determined by taking the average X and Y coordinates of all wolf relocations associated with the site. I used a generalized linear mixed effect model with a binomial distribution using the R package lme4 (Bates et al. 2015) to test if the four prey probability layers influenced the probability of wolves being found grouped or alone (n = 1,442). A second analysis only including kill sites from the 4 main prey species (e.g., moose, elk, white-tailed deer and beaver; n = 76) was completed to test if the effects of the prey RSFs influence wolf cohesion when wolves made a successful kill. In both of these models, pack ID was included as a random factor (Dickie et al. 2017). After testing

for the influence of availability, I used GLMs to test if prey size of captured prey at kill sites (when prey size was determined; $n = 75$) and scavenging sites ($n = 56$) influenced pack cohesion. Adult and yearling moose and elk were classified as large prey, while white-tailed deer, beavers, and moose and elk calves were classified as small prey. The beta coefficients for large vs small prey sizes were compared by converting them into odds ($\exp(\beta)$).

3.4 Results

3.4.1 Prey habitat Resource Selection Functions

Based on the constructed prey RSFs, moose avoided bogs, coniferous forests, open deciduous forests, open water, unpaved roads and rugged terrain (Appendix E; Table E2).

Beavers selected for marshes while avoiding mixed wood forests, coniferous forests and unmaintained trails (Appendix E; Table E2).

Elk in the winter selected for unmaintained trails while avoiding grasslands, mixed wood forests, bogs, coniferous forests, open deciduous forests, water bodies, streams and maintained trails. In the summer, elk significantly selected for grasslands, unmaintained trails and terrain ruggedness. Elk in the summer avoided mixed wood forests, marshes, bogs, open deciduous forests, water bodies, streams and maintained trails (Appendix E; Table E2).

White-tailed deer, in the winter selected for grasslands, marshes, open deciduous forests and maintained trails while they avoided mixed wood forests, bogs, streams, unmaintained trails and terrain ruggedness. In the summer, white-tailed deer selected for mixed wood forests, marshes, open deciduous forests, water bodies and maintained trails.

In the summer, white-tailed deer avoided grasslands, bogs, coniferous forests, unmaintained trails and terrain ruggedness (Appendix E; Table E2).

3.4.2 Pack cohesion in relation to prey availability at wolf clusters

A total of 1,442 sites were identified from the three packs followed from January 2016 to 2017. Results from the analysis at all clusters demonstrated a significant negative effect of beaver availability on wolf pack cohesion (β = -1.01; 95% CI = [-1.55, -0.48]) (Table 3.1; Figure 3.3). Moose availability had a marginally significant positive effect on wolf pack cohesion (β = 0.72; 95% CI = [-0.03, 1.48]). The availability of prey of intermediate body size within the system (e.g., white-tailed deer and elk) did not significantly affect the probability of pack cohesion (p = 0.199 and p = 0.736 respectively) (Table 3.1; Figure 3.3).

Pack cohesion at 76 kill sites was analyzed in relation to prey availability from January 2016 to 2017. No significant relationship was found between pack cohesion at kill sites and underlying prey availability of moose, elk, white-tailed deer, and beaver (p = 0.114; p = 0.636; p = 0.147; p = 0.334 respectively) (Table 3.1; Figure 3.4).

A post-hoc power analysis was conducted on the analysis investigating the influence of prey availability on pack cohesion at kill sites. The power analysis was conducted using the R package “pwr” (Champely 2018) to determine the required sample size to detect a significant effect (p = 0.05) for a generalized linear model of a similar effect size (ES) as the previous model including all the clusters (ES = 0.081) with a power level of 0.8. The resulting power analysis concluded that the sample size was not

large enough to detect an effect if one was present. A larger sample size could possibly yield significant results (Appendix F).

3.4.3 Pack cohesion in relation to killed and scavenged prey size

Pack cohesion at 75 kill sites was analyzed in relation to prey size found at the kill sites for the four main wolf prey species in RMNP. Pack cohesion was greater when larger prey species were killed, and wolves were more often alone at clusters where small prey were killed (Table 3.2; Figure 3.5). The odds of packs being cohesive did significantly differ between large prey species and small prey species as their 95% confidence intervals did not overlap. As for scavenging sites (n = 56), the odds of packs being cohesive did not significantly differ between large and small prey species, as their 95% confidence intervals did overlap. Additionally, the 95% confidence intervals of the odds of packs being cohesive for both prey sizes overlapped with 1, meaning that the odds of wolves being more or less cohesive at scavenging sites was not influenced by prey size at the sites (see Table 3.2 and Figure 3.5).

3.5 Discussion

An individual's decision to cooperate within a larger group or be less cohesive to maximise its own energy intake creates a situation where group cohesion fluctuates depending on external factors such as prey availability. This work provides an informative evaluation of the social dynamics of social predators facing multiple conflicts between the costs and benefits of energy acquisition, where wolf packs adjust their level of cohesion based on prey availability, responding differently according to prey size. Wolves increase their cohesiveness to capitalize on the increased availability of moose, a

large prey species, which would be more difficult to capture alone. Conversely, wolves decrease their cohesiveness and are more likely found alone – or in smaller groups – as the availability of a small prey species, beaver, increases since the energy acquired from such prey would seldom be enough for multiple individuals. However, analyses looking more closely at kill sites demonstrated a potential disconnect between where wolves find prey and where they capture prey since prey availability did not influence pack cohesion at kill sites, Rather, size of captured prey was a determinant factor in pack cohesion at kill sites, but not at scavenging sites.

Large prey are characterized as high risk and reward, as they are more difficult to capture (MacNulty et al. 2014), but provide more food for predators once subdued and captured. Therefore, when large species are present on the landscape, predators cooperate to capitalize on the opportunity. This was made apparent in this study, as I found evidence that wolves increase pack cohesion as moose availability increased when looking at all potential clusters. Although other studies have not looked at the relationship between cohesion and prey availability, some have demonstrated that kill success increased with increased pack members, more so with larger prey species (MacNulty et al. 2012, 2014). In certain instances, however, larger prey are not worth the increased risk, as an attempt at a kill may result in injury or death of the predator (Mukherjee and Heithaus 2013). For example, with the resurgence of bison in Yellowstone National Park, USA, wolves seem to not kill bison proportional to their availability, but rather focus their efforts on less risky, yet smaller elk (Tallian et al. 2017). A similar trend is seen in Scandinavia, where the kill rate of the more dangerous moose is primarily driven by the

abundance of the smaller alternative prey, roe deer (*Capreolus capreolus*) (Sand et al. 2016). The availability of a prey item characterized by the combination of increased cooperation requirements and higher food pay-off would encourage wolf packs to be more cohesive when smaller prey are less available.

The availability of small prey presents social carnivores with a more diverse decision set where competition between conspecifics outweighs the benefits of cooperation. The combination of the smaller energetic pay-off and the lesser risk involved with capturing smaller prey leads social carnivores to be less cohesive. This was shown in this work, where there was less pack cohesion where beaver were more available (Figure 3.3). Beaver are small prey that warrant less cooperation to be captured successfully, as capturing small prey require more cryptic and stealthy approaches (Gable et al. 2016). The smaller amount of food acquired from prey such as beaver when compared to large prey would deter individuals from sharing, which would further explain how the availability of small prey would reduce wolf pack cohesion. Similar trends are seen in Scandinavia, where pairs of wolves hunted the smaller prey, roe deer, more often than did packs, which hunted more moose (Sand et al. 2016). Beaver are an important prey species for wolves in the summer months when they are tending their young (Benson et al. 2015). Individuals may hunt beaver to capitalize on a less dangerous prey item in the summer that they can capture on their own, freeing other individuals to care for the young.

Although wolves are generalists and prey on multiple prey species within a system, they usually have a primary prey species based on abundance. In RMNP, moose are

currently the primary large prey species, while beaver are the primary small prey species. To this effect, moose are currently the most abundant ungulate species in RMNP. Studies have demonstrated that wolves respond to the habitat selection of their primary prey species (Lesmerises et al. 2012, Kittle et al. 2017, Zabihi- Seissan chapter 1 this thesis), and would therefore selecting for areas of high moose availability that is measured by moose habitat selection. Elk availability had no significant effect on pack cohesion when looking at all clusters although it would be classified as a large prey species. It requires a group size of four wolves to attain the maximum probability of capturing elk (MacNulty et al. 2012) in YNP, but it may be that wolves in RMNP are not responding to elk availability as current diet trends in these three wolf packs suggest that they are primarily feeding on moose (Appendix E; Figure E1). Increased cohesion would therefore be attributed to moose availability and not elk availability. White-tailed deer are considered a small prey species and wolves have been shown to capture other deer species at higher rates in pairs rather than in groups (Sand et al. 2016). However, the smaller number of white-tailed deer in RMNP (Parks Canada 2016a) and small numbers found at wolf kill sites (Appendix E; Figure E1) could explain the lack of effect of white-tailed deer availability on pack cohesion (Figure 3.3). The lack of selection for prey species, which may be apparent in the diet composition may explain the non-significance of the availability of certain prey species on pack cohesion.

The location where prey are encountered is not necessarily the same as where the prey are killed. Prey species are known to alter habitat selection to avoid predation (Sih 2005) and moose kill sites have been shown to cluster depending on habitat

characteristics (Montgomery et al. 2014). Therefore, there may be a fine-extent disconnect between where prey are most available (i.e., availability) and where wolves are able to capture them (i.e., catchability). This disconnect could explain why prey availability had no significant effect on pack cohesion when looking at clusters only associated with kill sites (Figure 3.4). Wolves are more cohesive based on prey availability in general but would have to capture prey in areas where they are vulnerable, which are potentially dissociated with their level of availability. The power analysis, however, demonstrated that a larger sample size would need to be required to potentially detect an effect of prey availability at the kill sites if there was one. Size of captured prey influenced cohesion at kill sites, where the odds of cohesion at large prey kill sites were higher than at small prey kill sites (Figure 3.5). The lower effect of prey availability compared to the effect of prey size at kill sites on wolf pack cohesion may be due to not all individuals in a pack being collared. The odds of cohesion at large prey kill sites suggests that wolves are more likely to be with conspecifics rather than alone at large prey kill sites. This is true in other systems, where kill site attendance was higher at kill sites with larger ungulates compared to smaller ungulates (Metz et al. 2011). The opposite is true at small prey kill sites, where wolves are more likely to be alone than with conspecifics.

Cooperation is required to increase the success rate in subduing larger prey (MacNulty et al. 2014); suggesting that cohesion is driven by the degree of danger or difficulty associated with subduing prey. The costs associated with the effort of capturing a large prey such as moose causes wolves to be more cohesive. Results from prey size at

kill sites reflect this; where wolves were more likely to be with other collared conspecifics at large prey kill sites compared to at smaller prey kill sites. Other studies have shown that wolves increase their likelihood of attending large carcasses compared to smaller ones (Metz et al. 2011) as large prey provide more food. However, my analysis at scavenging sites failed to find that relationship based on size of carcasses, suggesting that the driver of cohesion is driven by the cost of capturing large prey and not the amount of energy resulting in the capture. When scavenging, wolves are no longer constrained by the same requirements and visit these sites with or without conspecifics, their level of cohesion possibly dictated by the relative amount of food remaining or time of year (Barber-Meyer and Mech 2015), which is known to affect cohesion.

Here I show how the anticipation of having to cooperate to capture large prey or dissociate to capitalize on small prey shapes the fluid cooperative behaviour of wolves. My results showed strong support for the prediction that the availability of smaller prey (i.e., beaver) decreases the probability of pack cohesion (P2) and evidence to support the prediction that the availability of a large prey (i.e., moose) increases the probability of pack cohesion (P1). This was not the case with all prey species present on the landscape, but rather those that are probably targeted as primary prey in RMNP and that are harder to kill. The apparent disconnect between where prey are found and where they are killed suggests that large prey increases probability of pack cohesion at kill sites but not scavenging sites (P3), and this regardless of underlying prey availability. Wolves, as other social carnivores, need to consider the trade off between hunting cooperatively to ensure food acquisition and the cost of having to share the acquired food. In many

instances, social structure is important for energy acquisition and survival, and the stability of social units are intimately linked to the fitness of individuals. Within these stable social units, younger individuals benefit from older experienced individuals, while the later benefit from the survival of their offspring. Therefore, the process of cooperation is a critical link between population patterns resulting from underlying environmental factors such as resource distribution.

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Table 3.1. Coefficients, standard errors and p-values of fixed effect variables (prey availability) on the variation of pack cohesion at all clusters (*n* = 1,442) and at kill sites (*n* = 76) in three wolf packs in Riding Mountain National Park, Manitoba from January 2016 – January 2017. Both models consisted of generalized linear mixed models with a binomial distribution where cohesion was defined in two states, either a GPS-collared wolf alone (0) or accompanied by at least one other GPS-collared wolf (1). Pack ID was included as a random factor in both models. R-squares (marginal and conditional) for both models were also included.

Model	Variable	Coefficient	Std. Error	P-value	$R^2_{marginal}$	R^2_{cond}
Prey availability at all sites	Intercept	-0.720	0.343	0.036		
	Beaver	-1.015	0.272	< 0.001		
	WTD	1.293	1.007	0.199	0.016	0.075
	Elk	-0.137	0.406	0.736		
	Moose	0.723	0.384	0.060		
Prey availability at kill sites	Intercept	0.054	1.121	0.961		
	Beaver	-1.405	1.456	0.334		
	WTD	-14.970	10.326	0.147	0.110	0.154
	Elk	-0.901	1.906	0.636		
	Moose	2.993	1.895	0.114		

Table 3.2. Odds (with 95% confidence intervals) of wolves being cohesive in relation to prey size at kill sites (n = 75) and scavenging sites (n = 56) from three wolf packs in Riding Mountain National Park, Manitoba from January 2016 – January 2017. Models consisted of generalized linear models with a binomial distribution. Large prey were defined as adult moose and elk, while smaller prey were defined as beaver, white-tailed deer, and moose and elk calves. Cohesion was defined in two states, either a GPS-collared wolf alone (0) or accompanied by at least one other GPS-collared wolf (1). R-squares for both models were also included.

Model	Variable	Odds	Lower CI (95%)	Higher CI (95%)	R^2
Prey size at kill sites	Small prey	0.04	0.01	0.15	0.31
	Large prey	8.33	3.87	21.71	
Prey size at scavenging sites	Small prey	0.36	0.02	3.02	0.01
	Large prey	0.93	0.53	1.60	

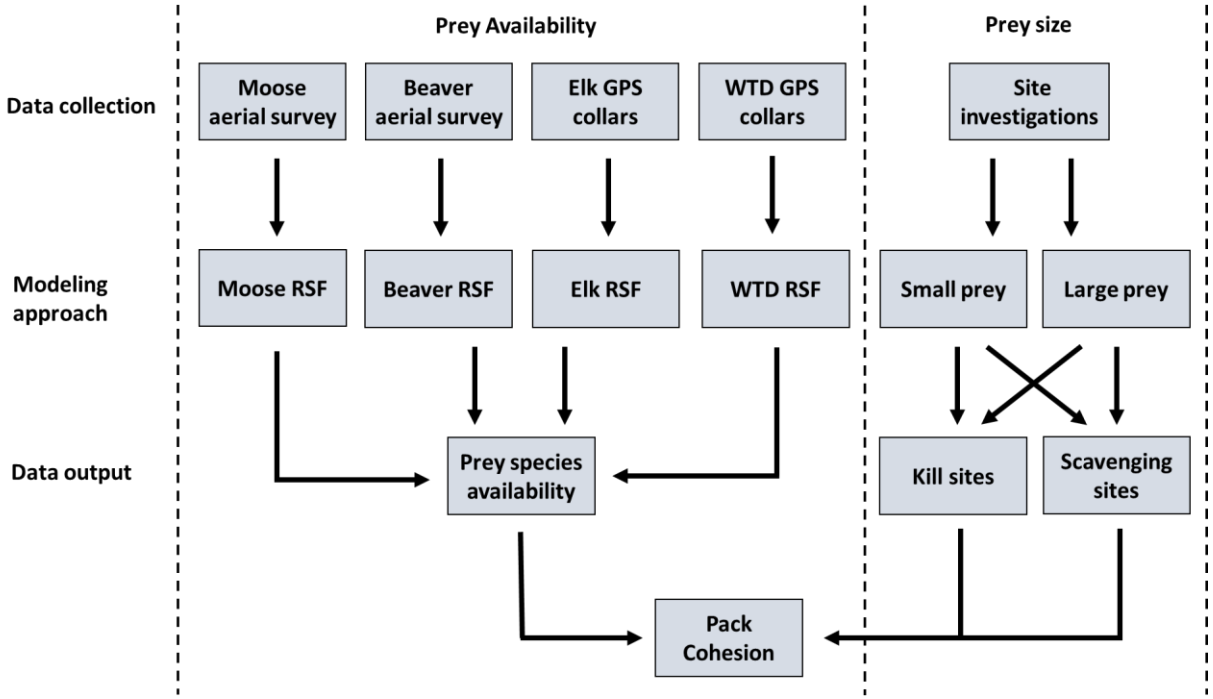

Figure 3.1. Flow chart of methods used to manipulate data and test the effect of prey species availability and prey size on pack cohesion in three wolf packs in Riding Mountain National Park, Manitoba, from January 2016- January 2017. Cohesion was defined in two states, either a GPS-collared wolf alone (0) or accompanied by at least one other GPS-collared wolf (1).

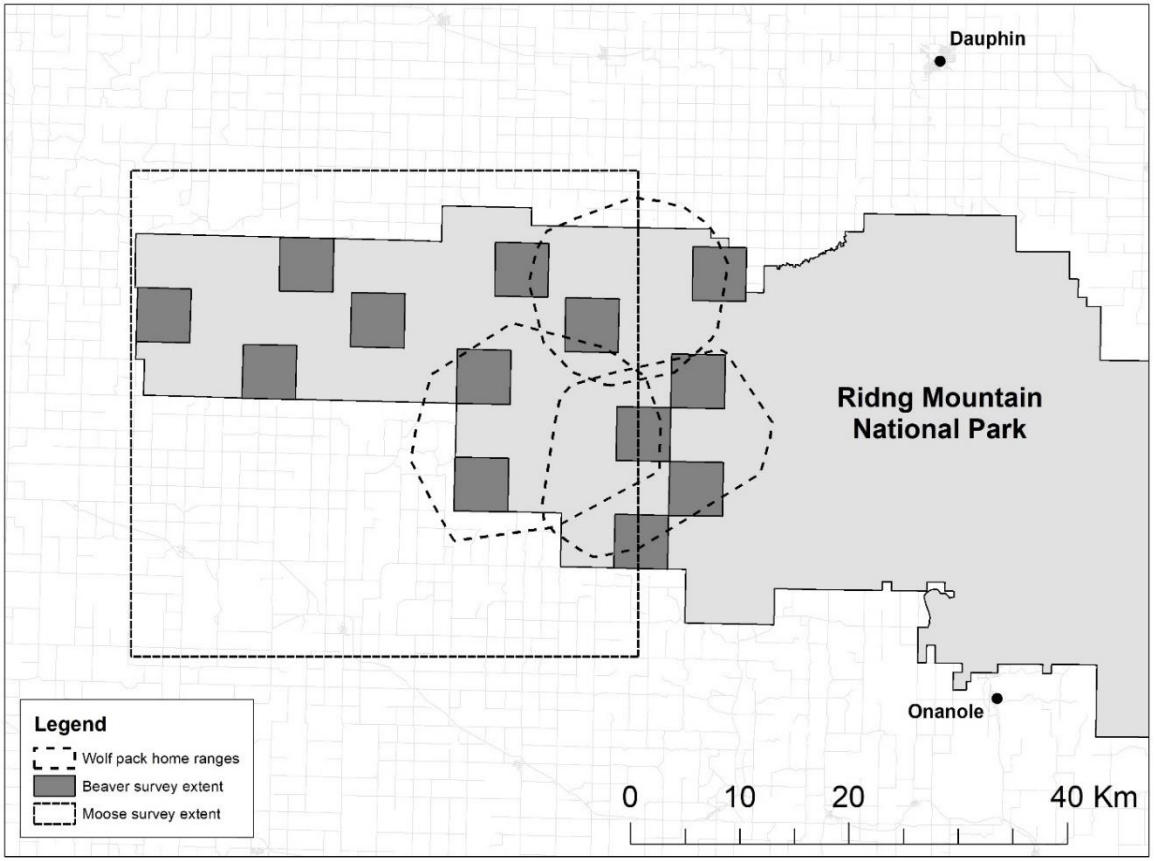

Figure 3.2. Map of the park border, moose and beaver survey extents, overlaid with three wolf pack home ranges found in the western portion of Riding Mountain National Park, Manitoba. The Baldy pack (south west; collared from January 2016 –

January 2017) and Gunn Lake pack (north; collared from January – June 2016) had each four out of five wolves collared. The Whitewater pack (south east, collared from January – June 2016) had three out of seven wolves collared.

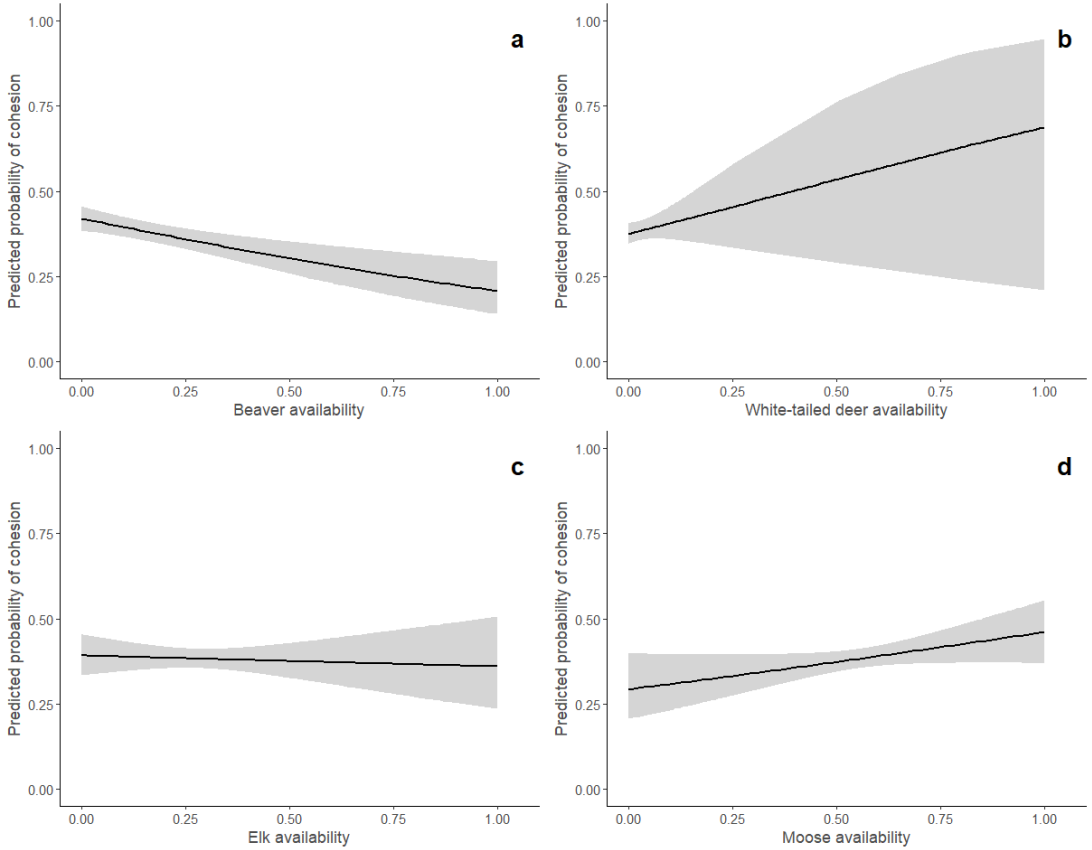

Figure 3.3. Model predicted probability of collared wolves being observed with collared conspecifics, i.e., cohesion, at GPS clusters (*n* = 1,442) for three wolf packs in Riding Mountain National Park, Manitoba (2016-2017) for each of four prey species: (a) beaver ($p < 0.001$), (b) white-tailed deer ($p = 0.199$), (c) elk ($p = 0.736$) and (d) moose ($p = 0.060$). Prey availability on the x-axes correspond to species RSF score which is a unitless value in geographic space. The model consisted

of a generalized linear mixed model with a binomial distribution where cohesion was defined in two states, either a GPS-collared wolf alone (0) or accompanied by at least one other GPS-collared wolf (1). Pack ID was included as a random factor in the model.

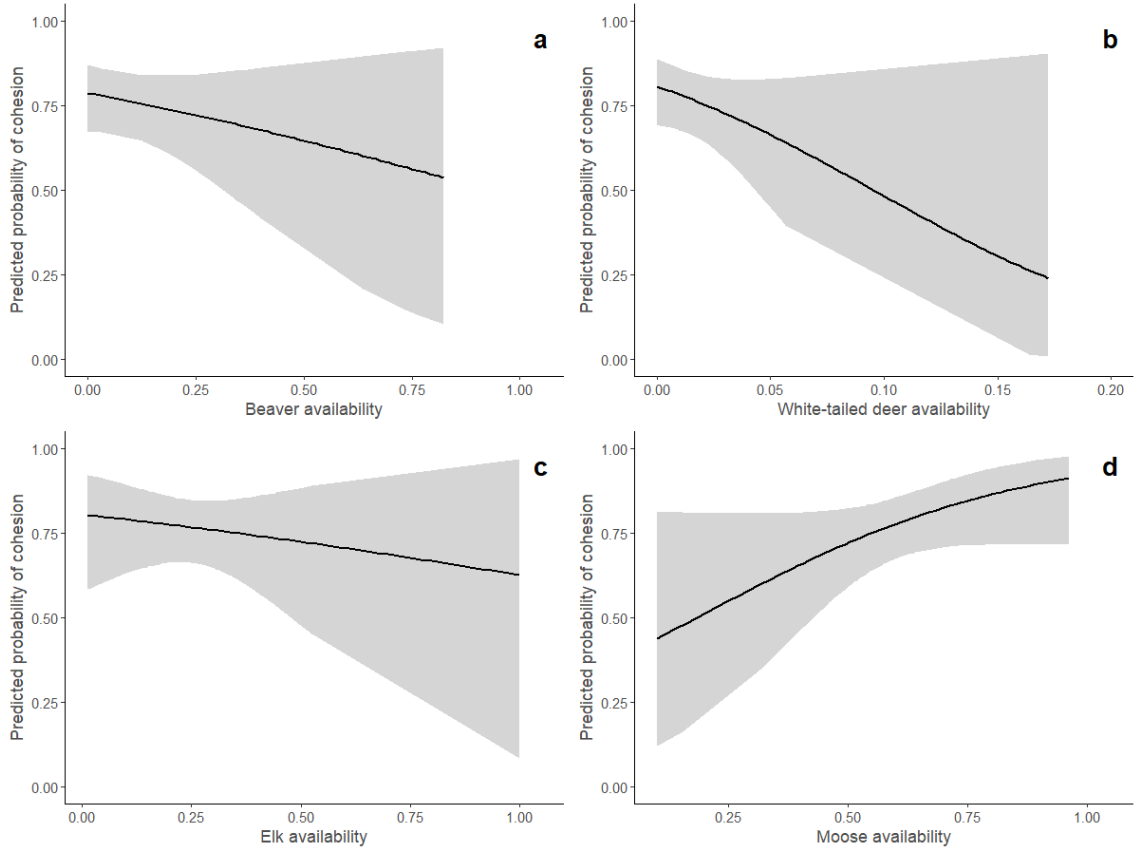

Figure 3.4. Model predicted probability of collared wolves being observed with collared conspecifics, i.e. cohesion, at known kill-site clusters (*n* = 76) for three wolf packs in Riding Mountain National Park, Manitoba (2016-2017) for each of four prey species: (a) beaver (p = 0.344), (b) white-tailed deer (p = 0.147), (c) elk (p = 0.636) and (d) moose (p = 0.114). Prey availability on the x-axes correspond to species RSF score which is a unitless value in geographic space. The model consisted

of a generalized linear mixed model with a binomial distribution where cohesion was defined in two states, either a GPS-collared wolf alone (0) or accompanied by at least one other GPS-collared wolf (1). Pack ID was included as a random factor in the model.

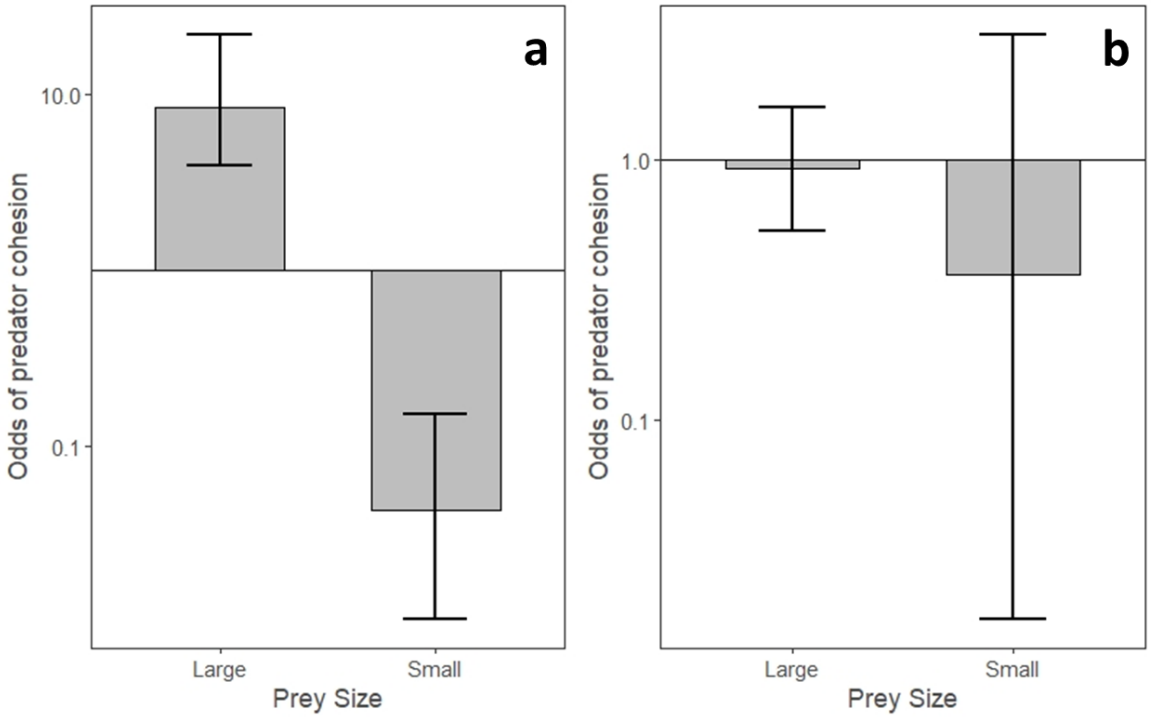

Figure 3.5. Odds (logs scale) of collared wolves being cohesive with collared conspecifics at clusters in relation to prey size at (a) kill sites (n = 75) and scavenging sites (n = 56). All observations were collected from three wolf packs in Riding Mountain National Park, Manitoba, January 2016 – January 2017. Each model consisted of a generalized linear model with a binomial distribution where cohesion was defined in two states, either a GPS-collared wolf alone (0) or accompanied by at least one other GPS-collared wolf (1).

CHAPTER 4: EPILOGUE

4.1 Conclusion

I have summarized in my thesis how an apex predator modifies its spatial and social environment in a natural system. Animals not only adjust their patterns of space use to maximize their energy intake, but in the cases of social carnivores that rely on cooperative hunting, shape their social environment by choosing to associate or dissociate with conspecifics to balance prey acquisition and their own energetic needs. The spatial distribution of resources, therefore, not only affects animal movement and space use (Roshier et al. 2008), but also their level of social aggregation.

Selective space-use allows generalist predators to adjust space use to changing prey abundances within a system, effectively enabling them to change their spatial environment. In this thesis, I demonstrated that wolves use the prey habitat tactic and the prey catchability tactic to maximize their chances of encountering and successfully capturing their primary prey species in RMNP (Riding Mountain National Park), i.e., moose. Wolves in RMNP used the same prey habitat tactic for elk, a secondary prey species, although to a lesser extent, suggesting a prey switch in comparison to previous studies in RMNP. Wolves also modified their level of cohesion in response to their primary prey species habitat preference (Chapter 3). I found strong evidence that wolves were more likely to be found alone in areas selected by their small prey, beaver. Further, my work suggested that wolves were together in areas where they might encounter moose. Further evidence of a prey switch from elk to moose is seen in wolf diet data from kill sites collected as a part of the RMNP wolf project (Prokopenko et al. unpublished

data); kill site investigations determined that wolves primarily killed moose and beaver, the most abundant large and small prey species in RMNP respectively. Potential switches in wolf diet have also been observed in other systems such as Scandinavia, where the selection for moose depended heavily upon the abundance of smaller more vulnerable roe deer (*Capreolus capreolus*; Sand et al. 2016). Previous concerns over the fate of wolves in RMNP with the decrease in the elk population (Sallows 2007) may be alleviated by the fact that wolves have switched to primarily feeding on moose. Wolves, like other generalist predators, are flexible when faced with changes in prey populations (Zlatanova et al. 2014), but managers and conservationists must be mindful of the impact a prey switch may have on other prey populations in the system and the subsequent change in space use tactics employed by predators.

Predator-prey relationships have historically been presented in terms of random encounters in well-mixed systems defined by speed and density of predator and prey (Holling 1966). I explored this framework by testing the prey abundance hypothesis (Chapter 2), for which I found no support. Realistically, predators must make decisions in the face of variations in natural systems and rely on other cues such as habitat to find their prey. The results from my thesis suggests that more weight should be given to factors such as prey habitat preferences and vulnerability in predator-prey studies (Tallian et al. 2017). The importance of prey habitat preferences and traits such as body size is highlighted in the response of wolves to the availability of options in RMNP. There are a variety of strategies to employ to hunt a variety of prey but as predicted, wolves selected

for moose habitat, which is their primary prey, but also selected for elk habitat, albeit to a lesser degree. This supports the original prey habitat hypothesis.

These decisions extend to pack social dynamics, specifically in response to prey availability on the landscape. Given the option of capturing large dangerous prey such as moose (Mukherjee and Heithaus 2013) or smaller more vulnerable prey, wolves exist within the tension of cooperating to capture prey (mitigating potential injury risk), but partitioning prey with conspecifics. To respond to this tension, wolves increased their level of cohesion with increasing size (danger) of prey most available in their vicinity (Chapter 3), supporting the initial hypothesis of Chapter 3 and also demonstrating the social implications of the supported prey vulnerability hypothesis from Chapter 2. Other systems have their own combinations of prey, demonstrating a multiplicity of options and resulting behaviour of wolves as they target different prey species based on availability and the landscape (Metz et al. 2012, Latham et al. 2013, Kittle et al. 2017). Similar trends are observable across systems, such as the use of prey habitat and the importance of small prey species in the summer (Metz et al. 2012). When presented with multiple options, predators rely on landscape features at fine spatial extents to find prey, and preserving key landscapes associated with prey habitat and vulnerability would ensure predator access to prey.

Although I presented complex processes within a predator–multi–prey system, some aspects of predator–prey interactions remain to be explored. For example, temporal variation (seasonally and daily) plays an important role in wolf social cohesion (Barber-Meyer and Mech 2015), diet (Metz et al. 2012, Gable et al. 2018), and prey availability.

Specifically, I demonstrated how wolves tracked large-bodied prey in the winter, however the distribution and behaviour of prey fluctuates over time such that prey may be distributed differently based on time of day or season. Wolves may therefore alter their space use tactics during the course of the day or seasonally to account for these changes. For example, wolves are most active when their prey are more active, their movement rate influencing wolf kill rates (Vander Vennen et al. 2016). Prey species such as elk adjust their habitat selection by avoiding areas of high probability of wolf kills when wolves are more active (Kohl et al. 2018). Likewise, wolves may alter their level of cohesion in response to temporal variation in prey distributions due to diel or seasonal shifts to offset the prey's anti-predator behaviours. Some prey species, such as beaver, are more active at night (Tevis 1950), and wolves may not only decrease their level of cohesion in beaver habitat, but also during periods when beavers are more active. This brings forth new variation in prey distributions that wolves need to deal with, which may be offset by wolves temporally adjusting their spatial and social environments. Factors unrelated to prey may be driving wolf cohesion and instead be related to other behaviours that vary over different temporal scales, such as resting (diel variation) or denning (seasonal variation). Further work is needed to better understand how wolves adjust their spatial and social environments on a diel and seasonal basis as prey are not only dynamic in space, but also in time.

In conclusion, the ideas explored throughout my work detail how wolves adjust their spatial and social environments based on underlying prey availability, which is intimately tied to habitat and landscape features. The spatial distribution of these

resources (i.e., prey) not only affects predator movement and space use (Roshier et al. 2008), but also predator social aggregation (Chapter 3). Wolves tracked their prey by matching their habitat selection with their prey, and subsequently adjusted their level of cohesion based on the habitat selection of their largest and smallest prey species. Wolves in RMNP went from a primarily wolf-elk to a wolf-moose dominated system. Following this switch, they altered behaviour and diet which highlights the flexibility of a top predator with the ability to regulate ecosystems (Ripple and Beschta 2012). Ensuring that wolves have access to key prey habitat where prey are also vulnerable will help maintain healthy predator populations, which will in turn exert important top down effects on the ecosystem (Ripple and Beschta 2004, Leroux and Schmitz 2015).

4.2 References

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APPENDIX A. CHAPTER 2 MAPS OF STUDY AREA

A.1 Map of wolf packs

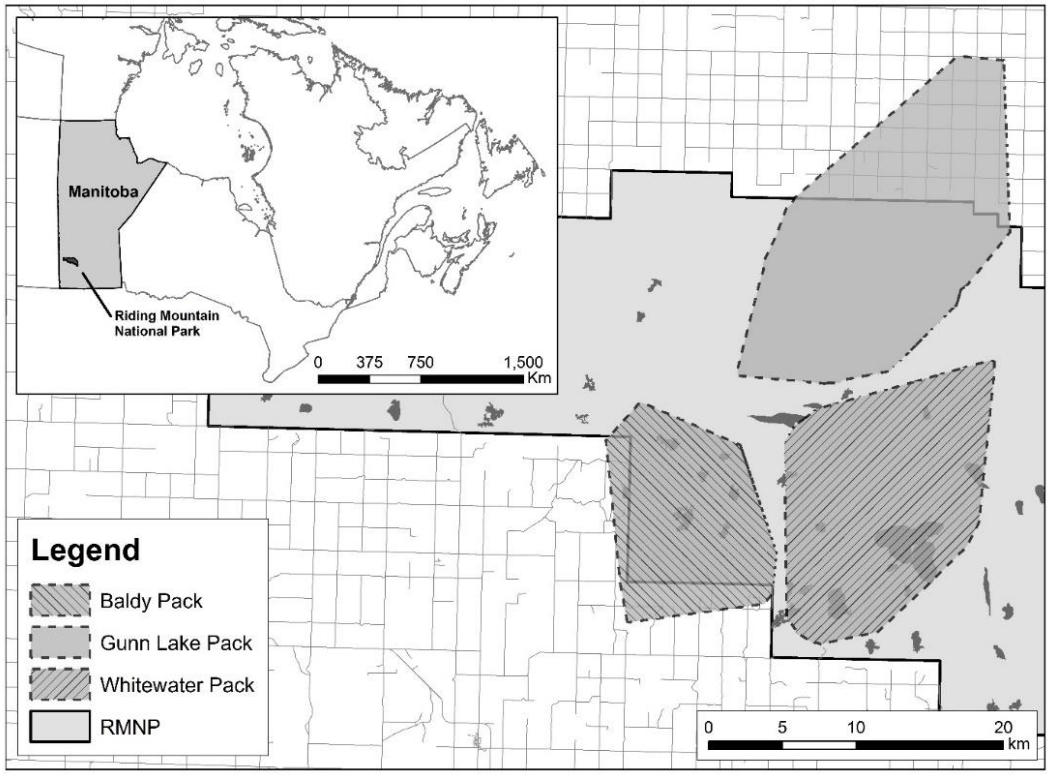

Figure A1. Map of the Riding Mountain National Park border, roads, overlaid with three GPS collared wolf pack home ranges (95% minimum convex polygons) found in the western portion of Riding Mountain National Park, Manitoba, Canada. From January-February 2016, the Baldy pack (south west) and Gunn Lake pack (north) each had three out five wolves collared while the Whitewater pack (south east) had three out of seven wolves collared. Dark polygons represent bodies of water.

A.2 Map of ungulate survey

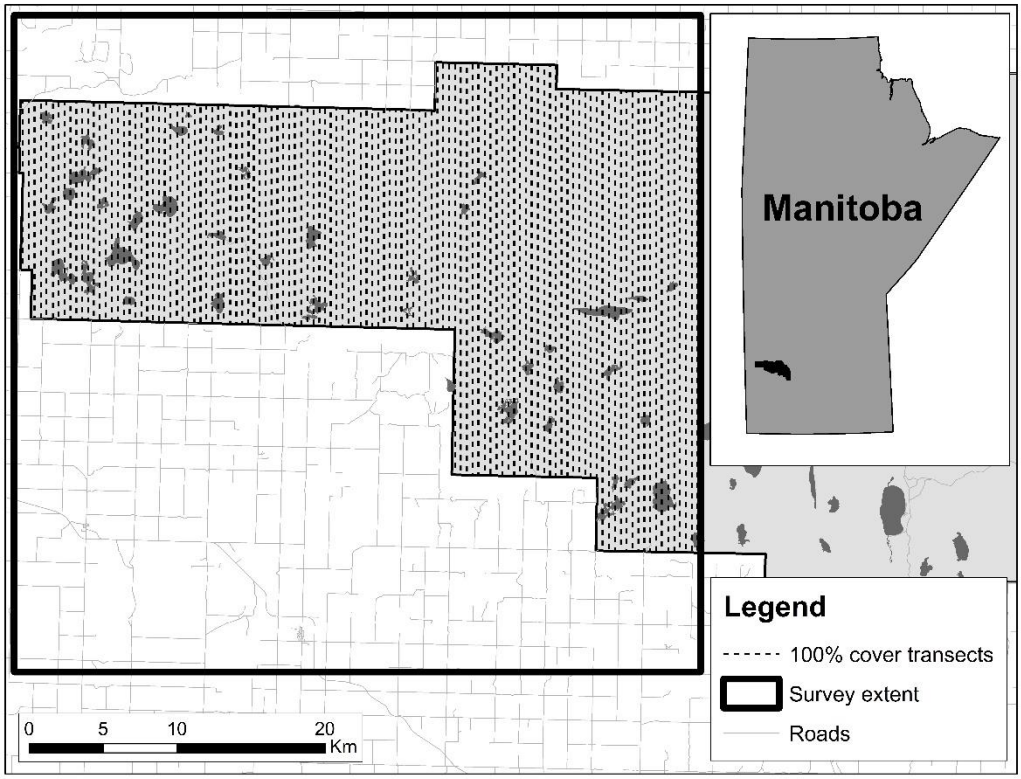

Figure A2. Map representing survey area and transects used during Parks Canada's 2016 100% cover winter ungulate survey where transects were flown 400m apart in Riding Mountain National Park, Manitoba, Canada (Parks Canada 2016). Dark polygons represent bodies of water.

A.3 References

Parks Canada. 2016. Riding Mountain elk / moose classified count survey and minimum population counts 2016. Riding Mountain National Park.

APPENDIX B. CHAPTER 2 DENSITY CORRELATION MATRIX

B.1 Density correlation matrix

A correlation matrix was used to ensure that the density distribution of moose and elk in 2016 is representative of the general winter distribution of these species in Riding Mountain National Park. The 2016 density data for moose and elk, measured using the Parks Canada ungulate survey (Parks Canada 2016a), were compared to the mean density distributions from the same survey from 2015 to 2017. The correlation matrix demonstrated that the 2016 elk density was correlated to the mean elk density (correlation coefficient = 0.65) and that the 2016 moose density was correlated to the mean moose density (correlation coefficient = 0.70).

	2016 elk density	2016 moose density	Mean elk density	Mean moose density
2016 elk density	**1**	**0.13**	**0.65**	**0.14**
2016 moose density	**0.13**	**1**	**0.11**	**0.7**
Mean elk density	**0.65**	**0.11**	**1**	**0.14**
Mean moose density	**0.14**	**0.7**	**0.14**	**1**

Figure B1. Correlation matrix comparing the 2016 moose and elk density distributions to the mean density distributions from 2015 to 2017 in the western portion of Riding Mountain National Park, Manitoba.

B.2 References

Parks Canada. 2016. Riding Mountain elk / moose classified count survey and minimum population counts 2016. Riding Mountain National Park.

APPENDIX C. CHAPTER 2 SUPPLEMENTARY FIGURES AND TABLES

C.1 Supplementary tables

Table C1. List of a priori models chosen for resource selection functions (RSF) to determine moose, elk and wolf habitat selection as well as moose and elk vulnerability based on habitat variables in Riding Mountain National Park, Manitoba. The RSF models consisted of generalized linear models with binomial distributions comparing used (where an animal was located) and available (where an animal could have been) points in space. The model with the smallest Akaike's information criterion (AIC) was selected as the best model for each set of models (shown in bold).

Model	Covariates*	*K*	Δ AIC	Δ AIC_{wt}	logLik
Moose habitat selection RSF					
4	**GL + MX + MR + BG + CN + OD + WT_D + PR_D + UR_D + RG**	**11**	**0.00**	**0.35**	**-2882.54**
6	GL + MX + MR + BG + CN + OD + WT_D + TM_D + TU_D + PR_D + UR_D + RG	13	0.01	0.35	-2880.53
3	GL + MX + MR + BG + CN + OD + WT_D + ST_D + PR_D + UR_D + RG	12	1.75	0.15	-2882.41
1	GL + MX + MR + BG + CN + OD + WT_D + ST_D + TM_D + TU_D + PR_D + UR_D + RG	14	1.77	0.15	-2880.40
7	GL + MX + MR + BG + CN + OD + WT_D + RG	9	28.40	0.00	-2898.74
5	GL + MX + MR + BG + CN + OD + WT_D + TM_D + TU_D + RG	11	29.73	0.00	-2897.40
2	GL + MX + MR + BG + CN + OD + WT_D + ST_D + TM_D + TU_D + RG	12	31.56	0.00	-2897.31
8	GL + MX + MR + BG + CN + OD + RG	8	44.42	0.00	-2907.76
Elk habitat selection RSF					
1	**GL + MX + MR + BG + CN + OD + WT_D + ST_D + TM_D + TU_D + RG**	**13**	**0.00**	**1**	**-50400.00**
2	GL + MX + MR + BG + CN + OD + WT_D + TM_D + TU_D + RG	12	52.05	0.00	-50427.02
3	GL + MX + MR + BG + CN + OD + WT_D + ST_D + RG	11	517.11	0.00	-50660.55
4	GL + MX + MR + BG + CN + OD + WT_D + RG	10	549.38	0.00	-50677.69
5	GL + MX + MR + BG + CN + OD + RG	9	1473.39	0.00	-51140.69
Moose vulnerability RSF					
4	**GL + MX + MR + BG + CN + OD + ST_D**	**9**	**0.00**	**0.49**	**-163.53**
5	GL + MX + MR + BG + CN + OD	8	1.25	0.26	-165.16
3	GL + MX + MR + BG + CN + OD + ST_D + ED_D	10	2.02	0.18	-163.53

2	GL + MX + MR + BG + CN + OD + ST_D + TM_D + TU_D + ED_D	12	4.75	0.05	-162.88
1	GL + MX + MR + BG + CN + OD + WT_D + ST_D + TM_D + TU_D + ED_D	13	6.34	0.02	-162.66
Elk vulnerability RSF					
5	**GL + MX + MR + CN + OD + ED_D + RG**	**9**	**0.00**	**0.62**	**-64.29**
4	GL + MX + MR + CN + OD + ST_D + ED_D + RG	10	1.93	0.24	-64.24
2	GL + MX + MR + CN + OD + WT_D + ST_D + ED_D + RG	11	3.94	0.09	-64.24
3	GL + MX + MR + CN + OD + WT_D + ST_D + RG	10	5.51	0.04	-66.03
1	GL + MX + MR + CN + OD + WT_D + ST_D + ED_D + RG + TM_D + TU_D	12	7.62	0.01	-64.06
Wolf habitat selection RSF					
2	**GL + MX + MR + BG + CN + OD + WT_D + ST_D + ED_D + RG**	**13**	**0.00**	**0.72**	**-10495.28**
1	GL + MX + MR + BG + CN + OD + WT_D + ST_D + ED_D + TM_D + TU_D + RG	15	1.85	0.28	-10494.21
3	GL + MX + MR + BG + CN + OD + WT_D + ST_D + RG	12	106.15	0.00	-10549.36
4	GL + MX + MR + BG + CN + OD + WT_D + RG	11	409.32	0.00	-10701.95
5	GL + MX + MR + BG + CN + OD + RG	10	414.65	0.00	-10705.61
6	GL + MX + MR + BG + CN + OD	9	839.76	0.00	-10919.16

* GL = grassland, MX = mixed wood forest, MR = marsh, BG = bog, CN = coniferous forest, OD = Open deciduous forest, WT_D = distance to water, ST_D = distance to stream, TM_D = distance to maintained trail, TU_D = distance to unmaintained trail, PR_D = distance to paved road, UR_D = distance to unpaved road, ED_D = distance to hard edge, RG = terrain ruggedness.

Table C2. The best grain at which each of these prey distribution metrics contributed to wolf space use was determined by comparing seven different models containing the average value of the prey metric within buffers of different sizes ranging from 30 m to 4 km. Model structure consisted of the prey metric at the tested grain size in addition to wolf and pack ID as random effects. The models were compared using Akaike's information criterion (AIC) and the model with the smallest AIC value was selected as containing the best grain at which the prey metric was describing wolf space use.

Model	Grain (m)	*K*	Δ AIC	Δ AIC_{wt}	logLik
Moose density	500	4	0.00	1.00	-10904.82
	1000	4	110.57	0.00	-10960.10
	250	4	148.15	0.00	-10978.90
	4000	4	168.43	0.00	-10989.04
	100	4	197.05	0.00	-11003.34
	2000	4	204.01	0.00	-11006.83
	30	4	206.07	0.00	-11007.85
Elk density	500	4	0.00	0.88	-11009.22
	250	4	6.04	0.04	-11012.24
	30	4	6.27	0.04	-11012.35
	100	4	7.07	0.03	-11012.75
	4000	4	9.89	0.01	-11014.16
	1000	4	11.25	0.00	-11014.84
	2000	4	12.21	0.00	-11015.32
Moose habitat selection	4000	4	0.00	1.00	-10949.42
	2000	4	55.41	0.00	-10977.13
	1000	4	78.40	0.00	-10988.62
	500	4	126.59	0.00	-11012.72
	250	4	131.01	0.00	-11014.92
	30	4	131.96	0.00	-11015.40
	100	4	132.04	0.00	-11015.44
Elk habitat selection	2000	4	0.00	0.98	-10976.77
	1000	4	7.63	0.02	-10980.58
	500	4	58.38	0.00	-11005.96
	4000	4	73.56	0.00	-11013.55
	250	4	74.54	0.00	-11014.03
	30	4	76.03	0.00	-11014.78
	100	4	77.09	0.00	-11015.31
Moose vulnerability	30	4	0.00	1.00	-10901.63

	100	4	71.46	0.00	-10937.36
	250	4	165.61	0.00	-10984.44
	1000	4	178.87	0.00	-10991.07
	500	4	200.89	0.00	-11002.08
	2000	4	211.50	0.00	-11007.39
	4000	4	223.78	0.00	-11013.52
Elk vulnerability	100	4	0.00	0.90	-10891.60
	30	4	4.83	0.08	-10894.02
	1000	4	8.24	0.01	-10895.72
	250	4	36.05	0.00	-10909.62
	500	4	45.92	0.00	-10914.56
	2000	4	88.53	0.00	-10935.86
	4000	4	120.37	0.00	-10951.79

Table C3. Table of covariates with β coefficient and p-values for top models selected from lists of a priori models for moose, elk and wolf habitat selection, as well as moose and elk vulnerability on the landscape. All models used data from winter 2016 collected in Riding Mountain National Park, Manitoba. Significant p-values ($p < 0.05$) are shown in bold.

	Model									
	Moose habitat RSF		Elk habitat RSF		Moose vulnerability RSF		Elk vulnerability RSF		Wolf habitat RSF	
Covariates*	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
Intercept	-3.71	**0.01**	-3.22	**<0.001**	-2.74	**<0.001**	-4.63	**<0.001**	-0.70	**<0.001**
GL	0.16	0.80	-1.65	**<0.001**	3.36	0.17	-2.13	0.73	-0.65	0.11
MX	-0.22	0.40	-0.16	**0.02**	0.41	0.58	0.14	0.91	-0.12	0.41
MR	-0.14	0.56	-0.21	**0.01**	-1.36	0.29	-2.31	0.37	-1.10	**<0.001**
BG	-3.95	**<0.001**	-1.94	**<0.001**	-0.70	0.83	-	-	-1.62	**<0.001**
CN	-2.51	**0.01**	-0.36	**0.05**	-9.64	0.08	3.05	0.39	1.39	**0.01**
OD	-1.52	**<0.001**	-0.23	**0.02**	0.98	0.57	-1.66	0.76	-0.25	0.23
WT_D	0.75	**<0.001**	2.18	**<0.001**	-	-	-	-	-0.25	**0.04**
ST_D	-	-	0.47	**<0.001**	-1.66	**0.05**	-	-	-1.65	**<0.001**
TM_D	-	-	0.22	**<0.001**	-	-	-	-	-	-
TU_D	-	-	-1.29	**<0.001**	-	-	-	-	-	-
PR_D	0.47	0.77	-	-	-	-	-	-	-	-
UR_D	2.26	**<0.001**	-	-	-	-	-	-	-	-
ED_D	-	-	-	-	-	-	-2.26	**0.04**	-0.84	**<0.001**
RG	-1.69	**0.04**	0.29	0.16	-	-	14.52	**0.01**	7.94	**<0.001**

* GL = grassland, MX = mixed wood forest, MR = marsh, BG = bog, CN = coniferous forest, OD = Open deciduous forest, WT_D = distance to water, ST_D = distance to stream, TM_D = distance to maintained trail, TU_D = distance to unmaintained trail, PR_D = distance to paved road, UR_D = distance to unpaved road, ED_D = distance to hard edge, RG = terrain ruggedness.

Table C4. Coefficients, standard errors and p-values of variables found in the top model looking at the effects of habitat and prey distribution on wolf space use (n = 9) in three wolf packs from January to February 2016 in Riding Mountain National Park, Manitoba, without interactions being considered into the model. Significant p-values ($p < 0.05$) are shown in bold.

Variable	Coefficient	St. Error	P-value
Intercept	-3.13	0.21	**< 0.001**
Grassland	-4.48	0.51	**< 0.001**
Mixed wood forest	-0.38	0.16	**0.02**
Marsh	-0.32	0.17	0.06
Bog	-1.14	0.49	**0.02**
Coniferous forest	5.20	0.62	**< 0.001**
Open deciduous forest	-0.41	0.25	0.10
Distance to water	-0.20	0.12	0.10
Distance to hard edge	-0.94	0.08	**< 0.001**
Terrain ruggedness	7.62	0.51	**< 0.001**
Moose habitat	1.07	0.13	**< 0.001**
Elk habitat	0.31	0.16	**0.05**
Moose density	-2.81	0.22	**< 0.001**
Elk density	-2.08	0.87	**0.02**
Moose vulnerability	5.99	0.39	**< 0.001**

* Distance to stream was omitted from the original wolf habitat RSF due to multicollinearity with prey variable.

C.2 Supplementary figures

	Grassland	Mixedwood	Marsh	Bog	Coniferous	Open deciduous	Distance to water	Distance to hard edge	Terrain ruggedness	Elk density	Moose density	Elk habitat	Moose habitat	Moose vulnerability
Grassland	1	-0.04	-0.15	-0.06	0.02	-0.02	0.03	-0.09	0.04	-0.03	0.07	0.03	-0.13	0.51
Mixedwood	-0.04	1	-0.06	0.11	0.46	-0.03	0.17	0	-0.02	-0.04	-0.05	-0.19	0.16	-0.06
Marsh	-0.15	-0.06	1	-0.02	-0.06	-0.03	-0.27	-0.3	-0.24	-0.01	-0.06	-0.31	0.06	-0.31
Bog	-0.06	0.11	-0.02	1	0.27	0.18	0.09	-0.07	-0.11	-0.01	-0.06	-0.2	-0.04	-0.15
Coniferous	0.02	0.46	-0.06	0.27	1	0.04	0.17	-0.06	0.1	-0.01	-0.03	-0.16	0.23	-0.31
Open deciduous	-0.02	-0.03	-0.03	0.18	0.04	1	0.07	0	-0.04	-0.04	-0.1	-0.14	-0.24	0.29
Distance to water	0.03	0.17	-0.27	0.09	0.17	0.07	1	0.16	0.24	0.02	0.1	0.33	0.25	0.14
)istance to hard edge	-0.09	0	-0.3	-0.07	-0.06	0	0.16	1	0.05	0.02	0.03	0.21	0.08	0.03
Terrain ruggedness	0.04	-0.02	-0.24	-0.11	0.1	-0.04	0.24	0.05	1	-0.01	-0.02	0.26	0.06	0.18
Elk density	-0.03	-0.04	-0.01	-0.01	-0.01	-0.04	0.02	0.02	-0.01	1	0.17	0.05	0.11	0
Moose density	0.07	-0.05	-0.06	-0.06	-0.03	-0.1	0.1	0.03	-0.02	0.17	1	0.06	0.15	0.04
Elk habitat	0.03	-0.19	-0.31	-0.2	-0.16	-0.14	0.33	0.21	0.26	0.05	0.06	1	0.4	0.27
Moose habitat	-0.13	0.16	0.06	-0.04	0.23	-0.24	0.25	0.08	0.06	0.11	0.15	0.4	1	-0.05
Moose vulnerability	0.51	-0.06	-0.31	-0.15	-0.31	0.29	0.14	0.03	0.18	0	0.04	0.27	-0.05	1

Figure C1. Correlation matrix showing the correlation coefficients between covariates found in the final 2016 winter wolf RSF model from Riding Mountain National Park, Manitoba, including habitat and prey distribution covariates. The highest correlation coefficient was between proportion of grassland and moose vulnerability at 0.51. All

correlations between variables, including prey distribution variables are below 0.6, which demonstrates an overall low correlation between covariates in the model.

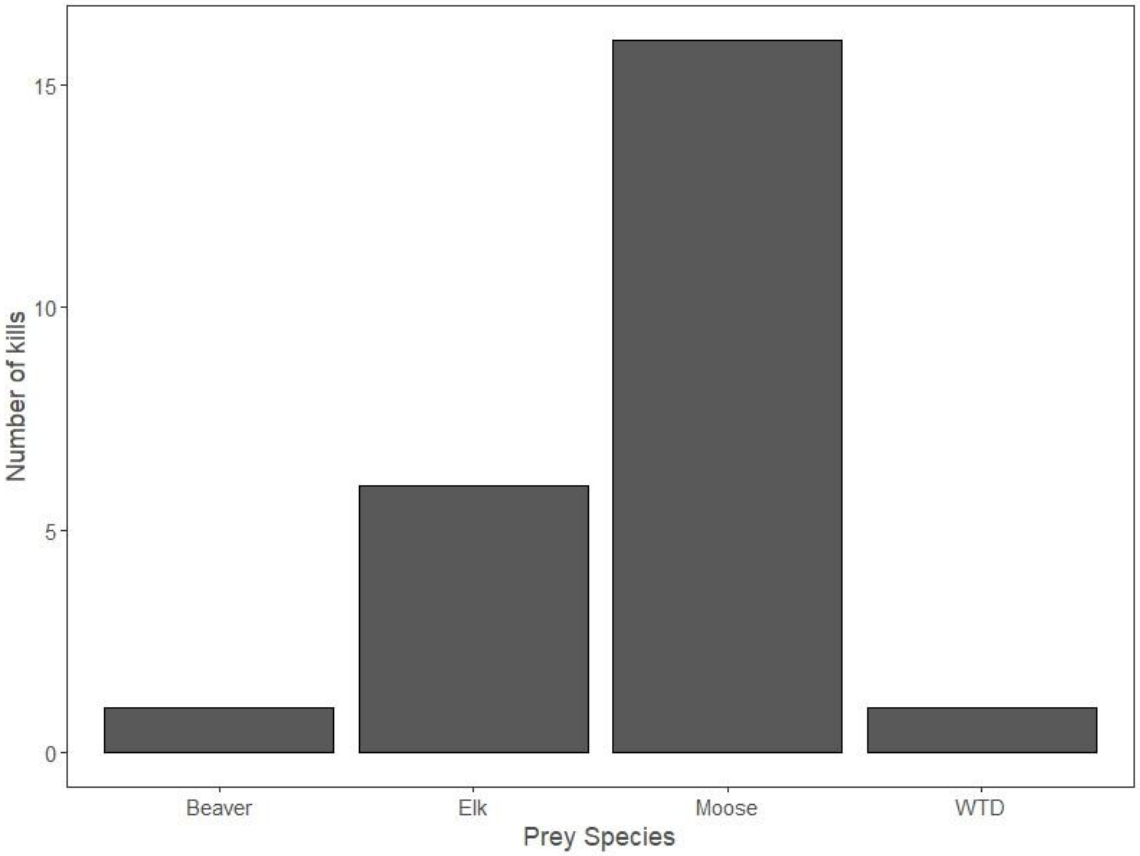

Figure C2. Number of kill sites found associated with three collared packs in Riding Mountain National Park, Manitoba, during the study period (January-February 2016). The majority of the species killed were moose and elk while only one beaver and white-tailed kills were identified.

APPENDIX D. CHAPTER 3 R CODE FOR MEASURE OF WOLF PACK COHESION

D.1 R code

R code used to calculate cluster attendance for 12 GPS collared wolves from January 2016 – January 2017 in Riding Mountain National Park (R Core Team 2016). The code determines cluster group membership by determining when individual wolf GPS point clusters overlap in space and time. Wolves present at the cluster are assigned a “1” in the attendance column output while wolves who were not present were assigned a “0”.

```
###  Wolf Cluster Attendance ----
# Author(s): Alec Robitaille, Sana Zabihi-Seissan
# Purpose: To determine cluster group membership based on time and
space
# Created on: February 8 2017
# Last updated: February 13 2017
# Inputs: Clusters
# Outputs: Cluster groups by spatial+temporal
# Copyright:

### Packages ----
libs <- c("data.table", "ggplot2", "lubridate", "igraph",
          "sp", "rgeos", "adehabitatHR","tidyr", "broom")
lapply(libs, require, character.only = TRUE)

### Input data ----
# Full Dataset
wolf.clusters <- fread("C:/Users/Sana/Google
Drive/Work/MUN/RData/Chapter
2/Input/Cluster_Centroids_NoDL.csv")[Clus_rad_m != 0]

### Pre-Processing ===

# Add datetime and roundtime, where roundtime is rounded by the hour
wolf.clusters[, c("startTime","endTime") := .(dmy_hms(paste(First_date,
First_time)),
                                              dmy_hms(paste(Last_date,
Last_time)))]

# Create a unique ID for each row
wolf.clusters[, rowID := seq(.N)]

### Functions ----
GroupClustersByTime <- function(dt){
  # Use foverlaps for interval overlaps
  overlap.clusters <- foverlaps(dt, dt, which = T,
                                nomatch = NA, type = "any")
```

```
  # Using igraph, create a graph from edge list (A->B), undirected
  grp.edges <- graph_from_edgelist(as.matrix(overlap.clusters),
                                   directed = F)

  # Time groups added from membership of graph from edgelist
  clusters(grp.edges)$membership
}

GroupClustersInSpace <- function(dt){
  # Make a spatial points data frame with the ids
  sp.points <- SpatialPointsDataFrame(dt[, .(X,Y)],
                                      proj4string =
CRS("+init=epsg:32614"),
                                      data = dt[, .(rowID)])

  # Buffer out the spatial points by the column buffer size
  bufs <- gBuffer(sp.points, dt[, Clus_rad_15],
                  byid = T, id = dt[, rowID])

  # Union (dissolve) all buffers to a single polygon feature
  un <- gUnaryUnion(bufs)

  # Disaggregate the non-touching buffers into individual features
  disag <- disaggregate(un)

  # Find membership to spatial groups over the buffers
  ov.r <- over(disag, sp.points, returnList=T)

  # # Return membership of spatial groups as data.table with list
unnested to rows
  sp.groups <- data.table(members = ov.r)[, spatialGroup :=
seq(members)]
  unnest(sp.groups, members)
}

### Spatial Groups ----
fstSpatial <- wolf.clusters[, GroupClustersInSpace(.SD),
                            .SDcols = c("Clus_rad_15", "rowID", "X",
"Y")]

wolf.clusters <- merge(wolf.clusters, fstSpatial, by = "rowID")

### Time Groups ----
# Set the key of data.table for foverlaps
setkey(wolf.clusters, startTime, endTime)

# Set time groups using function
wolf.clusters[, timeGroup := GroupClustersByTime(.SD), by =
spatialGroup]

### Spatial Check ----
wolf.clusters[, initialGroup := .GRP, by = .(spatialGroup, timeGroup)]

spatial.check <- wolf.clusters[, GroupClustersInSpace(.SD), by =
initialGroup,
                               .SDcols = c("Clus_rad_15", "rowID", "X",
"Y")]

spatial.check[, clusterGroup := .GRP, by = .(spatialGroup,
initialGroup)]
```

```
wolf.clusters <- merge(wolf.clusters, spatial.check[, .(rowID,
clusterGroup)], by = "rowID")

# Calculate mean X Y values
wolf.clusters[,meanx :=mean(X),by=clusterGroup]
wolf.clusters[,meany :=mean(Y),by=clusterGroup]

# Calculate first and last time for Whole Cluster
wolf.clusters[,FirstDayTime :=min(startTime),by=clusterGroup]
wolf.clusters[,LastDayTime :=max(endTime),by=clusterGroup]

#Calculate number of unique wolves at cluster
wolf.clusters[,WolfTotal :=length(unique(CollarID)),by=clusterGroup]

# Output the clusters
fwrite(wolf.clusters, "C:/Users/Sana/Google

Drive/Work/MUN/RData/Chapter 2/Output/Wolf_Cluster_Groups.csv")
```

D.2 References

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

APPENDIX E. CHAPTER 3 SUPPLEMENTARY FIGURES AND TABLES

E.1 Supplementary tables

Table E1. List of *a priori* models chosen for resource selection functions (RSF) to determine moose, elk and wolf habitat selection as well as moose and elk vulnerability based on habitat variables in Riding Mountain National Park, Manitoba. The RSF models consisted of generalized linear models with binomial distributions comparing used (where an animal was located) and available (where an animal could have been) points in space. The model with the smallest Akaike's information criterion (AIC) was selected as the best model for each set of models (shown in bold).

Model	Covariates*	*K*	Δ AIC	Δ AIC_{wt}	logLik
Moose RSF					
4	**GL + MX + MR + BG + CN + OD + RG + WT_D + PR_D + UR_D**	**11**	**0.00**	**0.35**	**-2882.54**
6	GL + MX + MR + BG + CN + OD + RG + WT_D + TM_D + TU_D + PR_D + UR_D	13	0.01	0.35	-2880.53
3	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D + PR_D + UR_D	12	1.75	0.15	-2882.41
1	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D + TM_D + TU_D + PR_D + UR_D	14	1.77	0.15	-2880.40
7	GL + MX + MR + BG + CN + OD + RG + WT_D	9	28.40	0.00	-2898.74
5	GL + MX + MR + BG + CN + OD + RG + WT_D + TM_D + TU_D	11	29.73	0.00	-2897.40
2	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D + TM_D + TU_D	12	31.56	0.00	-2897.31
8	GL + MX + MR + BG + CN + OD + RG	8	44.42	0.00	-2907.76
Elk summer RSF					
1	**GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D + TM_D + TU_D**	**13**	**0.00**	**0.83**	**-33324.43**
2	GL + MX + MR + BG + CN + OD + RG + WT_D + TM_D + TU_D	12	3.24	0.17	-33327.05
4	GL + MX + MR + BG + CN + OD + RG + WT_D	10	339.37	0.00	-33497.11
3	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D	11	341.23	0.00	-33497.04
5	GL + MX + MR + BG + CN + OD + RG	9	459.50	0.00	-33558.18
Elk winter RSF					
1	**GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D + TM_D + TU_D**	**13**	**0.00**	**1.00**	**-52199.75**
2	GL + MX + MR + BG + CN + OD + RG + WT_D + TM_D + TU_D	12	80.99	0.00	-52241.24
3	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D	11	524.31	0.00	-52463.90

4	GL + MX + MR + BG + CN + OD + RG + WT_D	10	575.63	0.00	-52490.56
5	GL + MX + MR + BG + CN + OD + RG	9	1462.21	0.00	-52934.85
WTD summer RSF					
1	**GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D + TM_D + TU_D**	**13**	**0.00**	**0.63**	**-27212.16**
2	GL + MX + MR + BG + CN + OD + RG + WT_D + TM_D + TU_D	12	1.09	0.37	-27213.70
3	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D	11	72.37	0.00	-27250.35
4	GL + MX + MR + BG + CN + OD + RG + WT_D	10	75.26	0.00	-27252.79
5	GL + MX + MR + BG + CN + OD + RG	9	94.05	0.00	-27263.19
WTD winter RSF					
1	**GL + MX + MR + BG + CN + OD + RG + WTD + STD + TMD + TUD**	**13**	**0.00**	**1.00**	**-39170.11**
2	GL + MX + MR + BG + CN + OD + RG + WT_D + TM_D + TU_D	12	411.25	0.00	-39376.74
3	GL + MX + MR + BG + CN + OD + RG + WT_D + ST_D	11	559.38	0.00	-39451.81
4	GL + MX + MR + BG + CN + OD + RG + WT_D	10	1063.11	0.00	-39704.67
5	GL + MX + MR + BG + CN + OD + RG	9	1063.90	0.00	-39706.06
Beaver RSF					
4	**GL + MX + BG + CN + OD + MR_D + WT_D + TM_D + TU_D**	**10**	**0.00**	**0.44**	**-704.93**
1	GL + MX + BG + CN + OD + MR_D + WT_D + ST_D + TM_D + TU_D	11	0.29	0.38	-704.06
5	GL + MX + BG + CN + OD + MR_D	7	3.39	0.08	-709.67
3	GL + MX + BG + CN + OD + MR_D + WT_D	8	4.14	0.06	-709.03
2	GL + MX + BG + CN + OD + MR_D + WT_D + ST_D	9	4.27	0.05	-708.08

* GL = grassland, MX = mixed wood forest, MR = marsh, BG = bog, CN = coniferous forest, OD = Open deciduous forest, WT_D = distance to water, ST_D = distance to stream, TM_D = distance to maintained trail, TU_D = distance to unmaintained trail, PR_D = distance to paved road, UR_D = distance to unpaved road, ED_D = distance to hard edge, RG = terrain ruggedness.

Table E2. Table of covariates with β coefficient and p-values for models selected from list of a priori models for moose, elk and wolf habitat selection, as well as moose and elk vulnerability on the landscape. Significant p-values ($p < 0.05$) are shown in bold. . Moose and beaver data were collected via an aerial survey in 2016. Elk data was collected via GPS-collared elk in 2016 and white-tailed deer data was collected via GPS-collared white-tailed deer in 2013. All data was collected in Riding Mountain National Park, Manitoba. Significant p-values ($p < 0.05$) are shown in bold.

	Model											
	Moose RSF		Elk summer RSF		Elk winter RSF		WTD summer RSF		WTD winter RSF		Beaver RSF	
Covariates*	Coef	P-value	Coef	P-value	Coef	P-value	Coef	P-value	Coef	P-value	Coef	P-value
Intercept	-3.714	**0.006**	-2.822	**<0.001**	-3.340	**<0.001**	0.894	**0.041**	-2.298	**<0.001**	-0.906	0.114
GL	0.155	0.801	0.939	**<0.001**	-1.438	**<0.001**	-1.456	**<0.001**	9.689	**<0.001**	0.911	0.508
MX	-0.221	0.402	-1.251	**<0.001**	-0.190	**0.006**	2.195	**<0.001**	-1.123	**<0.001**	-1.317	**<0.001**
MR	-0.142	0.555	-1.402	**<0.001**	0.116	0.102	1.209	**<0.001**	0.767	**<0.001**	-	-
BG	-3.952	**<0.001**	-3.333	**<0.001**	-1.628	**<0.001**	-2.143	**<0.001**	-4.117	**<0.001**	-1.680	0.311
CN	-2.508	**0.012**	-0.387	0.236	-0.541	**0.004**	-5.599	**<0.001**	0.394	0.154	-4.525	**0.014**
OD	-1.518	**<0.001**	-5.979	**<0.001**	-0.332	**<0.001**	5.111	**<0.001**	0.291	**<0.001**	0.643	0.451
WT_D	0.749	**<0.001**	0.855	**<0.001**	2.100	**<0.001**	-0.612	**<0.001**	0.137	0.183	-0.252	0.449
ST_D	-	-	0.176	**0.022**	0.571	**<0.001**	0.148	0.079	1.486	**<0.001**	-	-
TM_D	-	-	2.174	**<0.001**	0.329	**<0.001**	-1.047	**<0.001**	-0.777	**<0.001**	0.139	0.776
TU_D	-	-	-0.591	**<0.001**	-1.294	**<0.001**	0.261	0.004	1.849	<0.001	1.219	**0.006**
PR_D	0.465	0.766	-	-	-	-	-	-	-	-	-	-
UR_D	2.260	**<0.001**	-	-	-	-	-	-	-	-	-	-
MR_D	-	-	-	-	-	-	-	-	-	-	-1.514	**<0.001**
RG	-1.689	**0.035**	1.586	**<0.001**	0.228	0.270	-1.221	**<0.001**	-2.562	**<0.001**	-	-

* GL = grassland, MX = mixed wood forest, MR = marsh, BG = bog, CN = coniferous forest, OD = Open deciduous forest, WT_D = distance to water, ST_D = distance to stream, TM_D = distance to maintained trail, TU_D = distance to unmaintained trail, PR_D = distance to paved road, UR_D = distance to unpaved road, MR_D = distance to marsh, RG = terrain ruggedness.

E.2 Supplementary figures

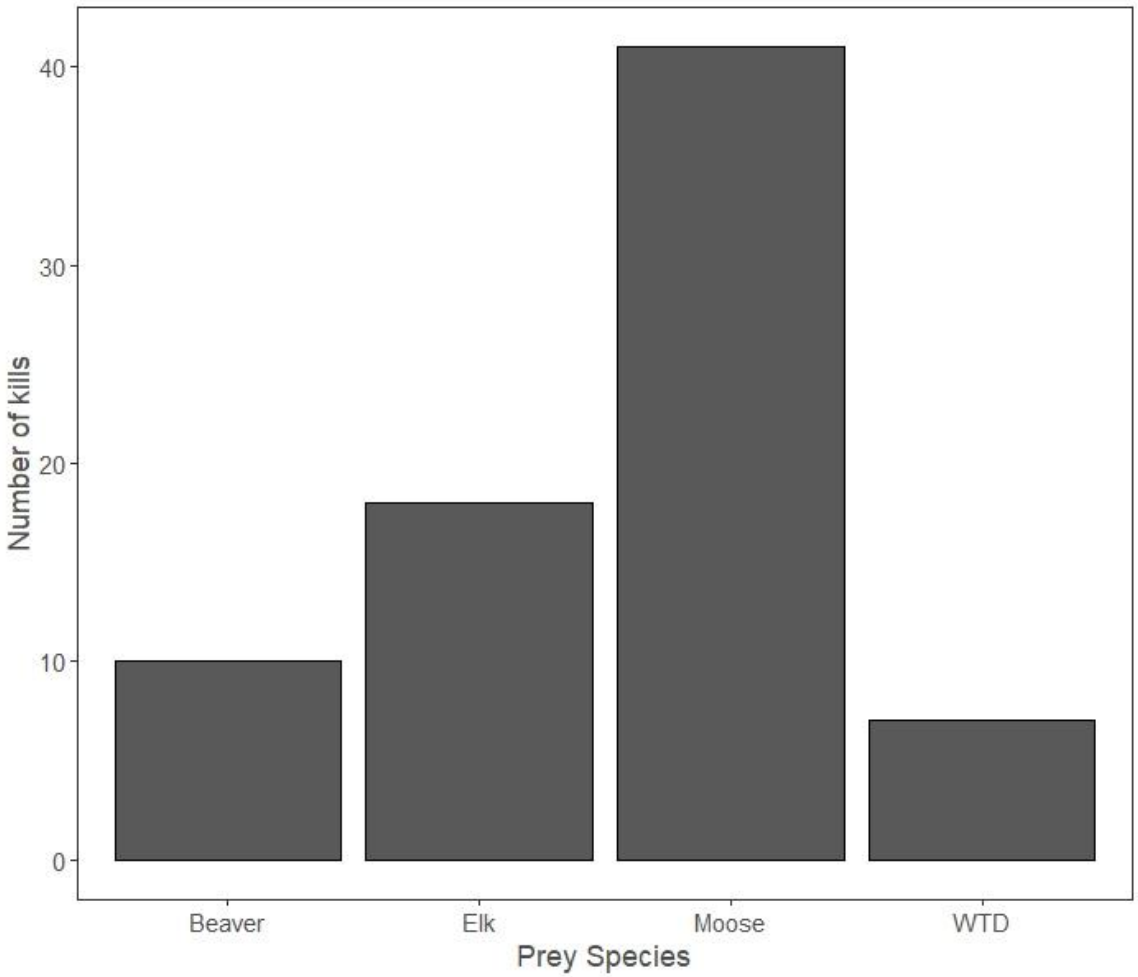

Figure E1. Breakdown by species of the n = 76 kill sites of the four main prey species (beaver, elk, moose and white-tailed deer) of wolves in Riding Mountain National Park, Manitoba that were found between January 2016 – January 2017 based on cluster investigations of three wolf packs.

APPENDIX F. CHAPTER 3 POWER ANALYSIS

F.1 Analysis

A power analysis was conducted using the package "pwr" (Champely 2018) in the statistical software R (R Core Team 2016). The effect size was estimated by using the conditional r^2 of the model looking at the effect of prey availability on wolf pack cohesion at all the clusters (conditional $r^2 = 0.075$).

To calculate required sample size, the following parameters were required:

```
u (number of parameters) = 4
f2 (effect size) = (r² / 1 – r²)
            = 0.081
sig.level (significance level) = 0.05
power = 0.8
```

Calculate required sample size:

```
pwr.f2.test(u=4,f2=(0.075/(1-0.075)),sig.level=0.05,power=0.8)
Multiple regression power calculation

              u = 4
              v = 147.0213
             f2 = 0.08108108
      sig.level = 0.05
          power = 0.8
```

Calculate sample size:

```
n = u + v + 1
n = 4 + 147 + 1
n = 152
```

F.2 References

Champely, S. 2018. Basic functions for power analysis. CRAN:1–22.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.